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BRYOLOGICAL PAPERS

II. THE ORIGIN OF THE CUPULE OF MARCHANTIA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 120

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(WITH FOURTEEN FIGURES)

The study of the cupule of Marchantia has evidently been confined to the later stages of its development, and especially to the origin of the gemmae and the order of cell division in them. Nowhere have we been able to find any account of the origin of the cupule, and the earlier stages of its development seem to have escaped observation. Its homology with other structures in the upper part of the thallus has apparently been a matter of speculation rather than of investigation. Thus, CAMPBELL casually remarks[1] that the gemma cup is apparently a specially developed air chamber, but gives no details and adduces no evidence therefor.

Although Marchantia has been much investigated and indeed has been long a favorite subject for instruction in laboratories, KNY seems to have been the first to examine any of the early stages of development of the cupule itself. This he did for the purpose of illustrating the development of Marchantia on his charts and describing the same in the accompanying text.[2] But he does not show or describe the origin of the cupule; the earliest stage referred to corresponds roughly to our *fig. 10*, when it has become a rather deep pit.

Our studies upon the origin of the air chambers in Marchantiales[3] suggested to us an inquiry into the origin of the cupule, to determine

[1] CAMPBELL, D. H., Mosses and ferns, 2d ed. 44. 1905.

[2] KNY, L., Wandtafeln. Ser. III, *pl. 84*, text p. 366.

[3] BARNES AND LAND, The origin of air chambers. BOT. GAZETTE **44**:197–213. 1907.

whether it could possibly be homologous with an air chamber. From an a-priori consideration of the general character of the cupule and the air chamber this idea commended itself to us both. The walls of the cup, especially the thin, lobed margin, seemed to correspond very well with the epidermal roof of the air chamber, opened wide instead of having only a narrow orifice. The gemmae, borne upon a single cell arising from the floor of the cup, might well be

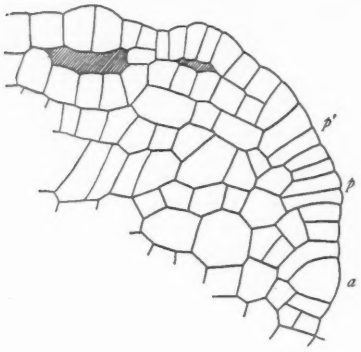

FIG. 1.—Early stage of cupule; *p*, *p'*, undivided cells, primordia of two (?) gemmiparous areas; *a*, apical cell; air chambers shaded.

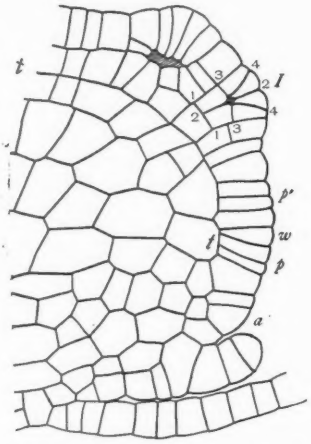

FIG. 2.—Early stage of cupule; *p*, *p'*, as in *fig. 1*; *w*, probably a rim cell between two gemmiparous areas; *a*, apical cell; *t*, *t*, line showing tissues of thallus involved in a cupule.

only a modified form of the chlorophyllose filaments of the air chamber. So natural and neat did the homology appear, that the brief prior statement of it by CAMPBELL (*l. c.*) was discovered with a distinct sense of disappointment when we began to look into the literature. But evidence for this homology could not be found therein, and against it was to be put the fewness of the cupules, their limitation to the median line, where the air chambers are least developed, and the fact that the gemmiparous region covers many times the area of an air chamber. The matter evidently needed examination. Actual observation of the origin of the cupule speedily dissipated all

notions of its homology with an air chamber, as we now proceed to show.

Abundant fresh material was at hand from thrifty plants of *Marchantia polymorpha*, grown under glass by Mr. JOHN COOK, the skilful gardener of the department, who has taken much pains with the cultivation of Hepaticae. Being transferred directly from the

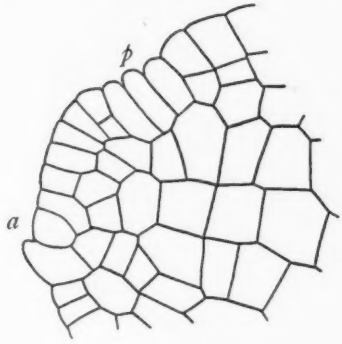

FIG. 3.—Gemmiparous area (*p*) outgrown by adjacent tissues.

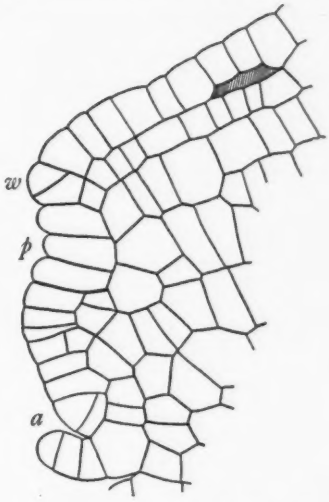

FIG. 4.—Stage nearly as in *fig. 3*; *w*, a rim cell cutting off the primordium of a lobe of the cupule.

cultures to the fixing fluids, the material was in exceptionally good condition.

Our figures show usually only the cell walls, the perfectly preserved contents being omitted for the sake of clearness. Mitotic figures were common, showing that the cells were in active growth. The figures are of longitudinal sections, except *fig. 13*, are all drawn to the same scale, and having been reduced one-half are now magnified about 625 diameters.

Longitudinal sections through the apex of gemmiferous plants show, as near to the apical cell as the third segment, a differentiation in the cells which are to form the gemmiparous area. Instead of

dividing by several successive periclinal walls, as most of the segments promptly do, the superficial parts remain for some time conspicuously undivided (*p*, *p'*, *fig. 1*), and so are distinguishable by their depth. In particular it is the final periclinal divisions that fail. This will be more evident by following the usual segmentation of the mother cell of an air chamber. In *fig. 2*, the young air chamber *I* originated as usual in a cell which underwent one periclinal division,

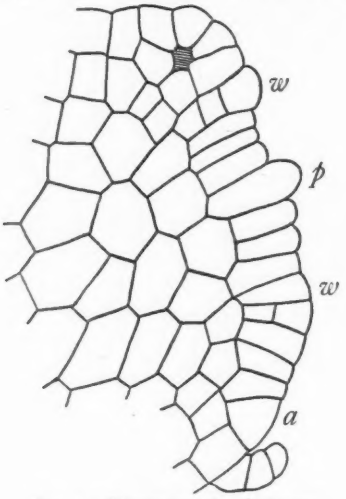

FIG. 5.—Elongation of a single gemmiparous cell (*p*); *w*, rim cells, the posterior oldest and most advanced in division.

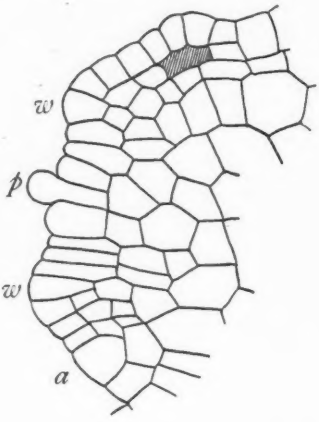

FIG. 6.—A somewhat later stage than *fig. 5*.

forming the wall *1*, *1;* then an anticlinal one (*2*, *2*); these two surface cells each divided periclinally (*3*, *3*), and cleavage occurred at the junction of walls *2* and *3*. (The curved anticlinal walls, *4*, *4*, succeeded the cleavage.) It is the divisions *1*, *1*, and *3*, *3*, or only the latter, which do not appear in the gemmiparous areas (*p*, *p'*).

The relative extent of the area which these undivided cells cover, and the occurrence of somewhat different cells (*w*) between them, make it not unlikely that in *figs. 1* and *2* the primordia of two cupules are laid down in close succession; but of this we cannot be sure.

The failure of the gemmiparous cells to divide allows their neigh-

bors to outgrow them, so that they can soon be located by the depression of the surface, as well as by their form and size (*p*, *fig. 3*). The depression, however, is not always well marked at this stage (cf. *fig. 5*). The contents, too, are sometimes distinctive, a glandular appearance being not infrequently noticeable; but as all the cells thereabouts are rich in protoplasm, this feature is not very striking.

The next step in development is the prolongation of one or more

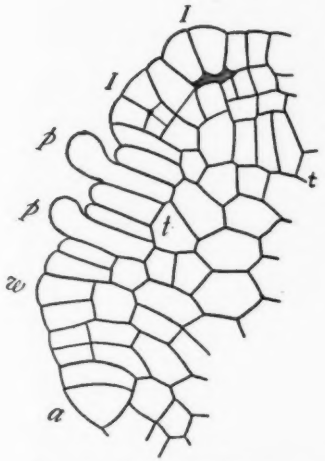

FIG. 7.—Two gemmiparous cells elongated; *I*, young air chambers; *t*, *t*, as in *fig. 2*.

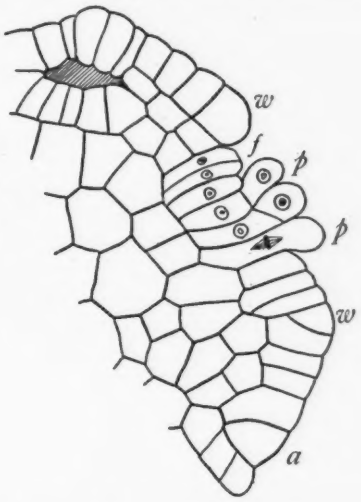

FIG. 8.—Further elongation and first division of gemmiparous cells (*p*, *p*); in *f* longitudinal division; *w*, rim cells.

of the gemmiparous cells into papillae (*p*, *figs. 5, 6*), and simultaneously the further upgrowth of the cells at the rim of the depression, and first on the posterior margin (*w*, *figs. 4, 5, 6*). The free ends of the papillose extensions quickly enlarge (*figs. 7, 8*) and doubtless secrete some of the mucus in which the whole apical region is enveloped. Certain of the cells that form the rim divide obliquely (*w*, *figs. 4, 8*). Probably the cells thus cut off are the primordia of the thin lobes, which are so marked a feature of the mature cupule; for even in this early condition the rim becomes scalloped.

After some further extension and enlargement, the gemmiparous

cells divide transversely (*p*, *p*, *fig. 8*), and soon another division occurs (*p*, *fig. 9*), by which three cells are formed, a basal cell (*b*), a stalk cell (*s*), and a gemma cell (*g*). The latter continues to divide in the

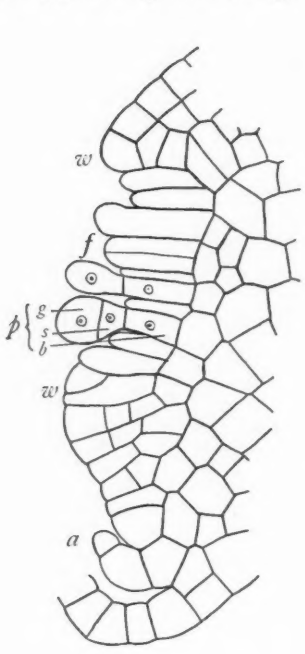

FIG. 9.—Progressing transverse (*p*) and longitudinal (*f*) division of gemmiparous cells; the former producing a basal cell (*b*), a stalk cell (*s*), and a gemma cell (*g*).

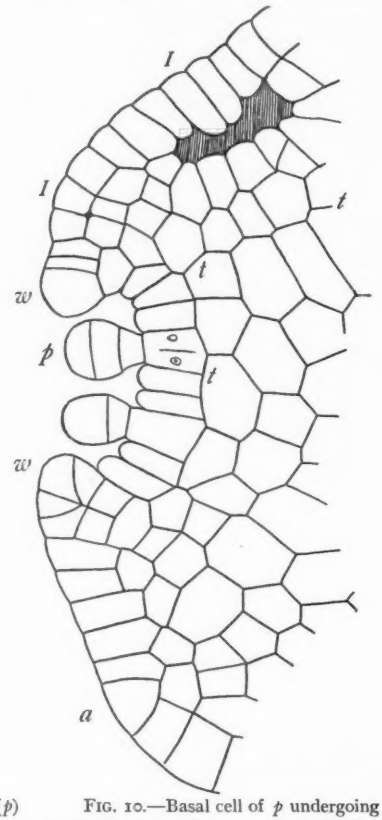

FIG. 10.—Basal cell of *p* undergoing longitudinal division; *w*, much further developed and depression deepened; *I*, young air chamber; *t*, *t*, *t*, shows relation of cupule and air chamber.

fashion frequently described and figured (cf. also *figs. 11*, *12*, *13*), and finally produces the gemma. The stalk cell undergoes no further division, but the basal cell divides longitudinally at least once (*p*, *fig. 11*). Later it may undergo repeated division, producing new

gemmiparous cells, so that each basal cell ultimately becomes the center of a group.

As the primordium of a cupule grows older, the number of gemmiparous cells forming its floor is increased by longitudinal (anticlinal) divisions (*f*, *figs. 8, 9*). The new floor cells so produced grow into

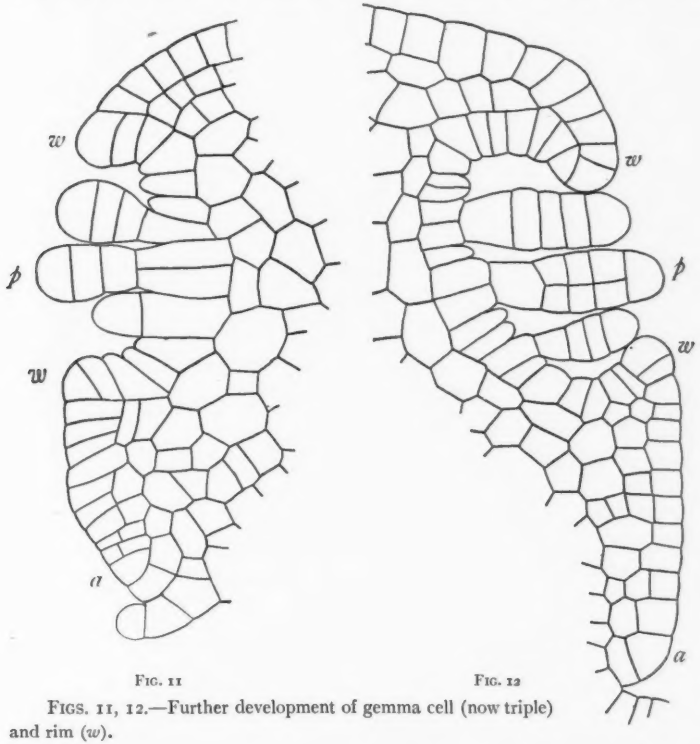

FIG. 11 FIG. 12

FIGS. 11, 12.—Further development of gemma cell (now triple) and rim (*w*).

papillae and soon produce gemma cells. Thus the gemmiparous area is increased in two ways: by the anticlinal division of the primordial cells, and by a similar division of basal cells that have borne or are bearing gemmae. The tissues adjacent grow rapidly, leaving the floor of the cupule soon far below the general surface (*fig. 12*), and the rim continues to outgrow the developing gemmae, which are embedded in mucus. The antero-posterior diameter of the young

cupule is less than the transverse diameter, as shown by *figs. 12* and *13*, which represent respectively longitudinal and transverse sections through cupules of about the same age.

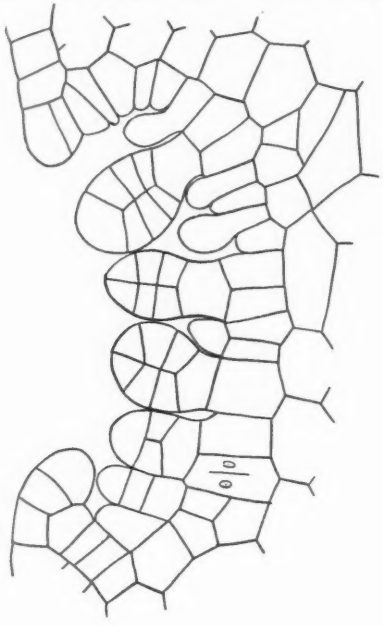

FIG. 13.—Transverse section of a cupule about the same age as *fig. 12*.

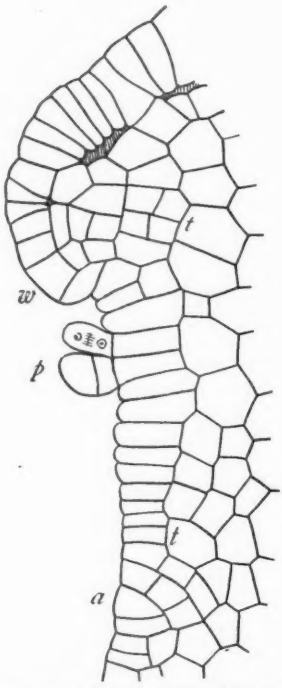

FIG. 14.—Origin of cupule of Lunularia; *p*, gemmiparous cells elongated and dividing; rim (*w*) developed only on posterior margin; *I*, young air chamber.

It is not necessary to follow the history of the cupule further, for it is a familiar object in all laboratories of instruction and has been well described.

The cupule of Lunularia has also been investigated sufficiently to show that its origin is essentially the same as that of Marchantia (*fig. 14*), except that the development of the rim takes place only on the posterior side of the gemmiparous region, which is also far more extensive. In some cases, late in development, a slight anterior

elevation continues the line of the posterior rim and so suggests the circular cup of Marchantia.

The superficial origin of the gemmae is thus perfectly clear. They cannot be considered as in any sense homologous with the chlorophyllose filaments of an opened air chamber, nor has the cup any relation to the epidermal roof. The thicker part of it *contains* air chambers, and the thin part is simply a scalelike outgrowth of the epidermis. The difference between an air chamber and a cupule becomes especially striking when a cupule originates near an air chamber, as shown in *figs. 2, 7, 10, 14,* at *I*. Then, although the gemmiparous cells are seen to be superficial, they evidently represent cells that otherwise might produce not only the roof, filaments, and floor of an air chamber, but also a considerable portion of the thallus beneath the air chamber. In *figs. 2, 7, 10,* the line, *l, l,* can be followed clearly, showing how deeply the gemmiparous cells involve the tissues of the thallus. It is not surprising, therefore, that the gemma cup, though of superficial origin, is a depression in the thallus, and that air chambers clothe its sides.

Incidentally we may add that the origin of the gemmiparous cells, as herein shown, precludes our acceptance of GOEBEL'S conception that in Marchantia the gemmae are homologous with "slime papillae."[5] The formation of mucus cannot be considered as a special function of any particular cells, though the so-called slime papillae have the name of "secreting" it. In fact young cells of very different origin and fate form mucus, and it is doubtful if any of the younger ones fail to form it. These "papillae" are purely superficial organs, and scarcely agree with the gemmiparous cells in anything except that at one time both project above the surface. How can the latter, which involve so considerable a part of the thallus, corresponding, as above shown, to the whole air chamber region and two or more layers of cells below it, be properly likened to such transient and superficial outgrowths as the "slime papillae"? To pronounce the two homologous throws no real light upon the nature of the gemmae, for the production of which there is such early and striking preparation.

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[5] GOEBEL, K., "Die Brutknospe von Marchantia und Lunularia kann auch als einer Schleimpapille homolog betrachten werden." Archegoniatenstudien XII. Flora **98**:314. 1908.

EMERGENCE OF LATERAL ROOTS[1]

RAYMOND H. POND

(WITH THREE FIGURES)

Our present conception of the method of emergence of lateral roots is based upon the elaborate exposition of the process made by VAN TIEGHEM in 1891. Since that time I am unable to find any record of emphatic disagreement with VAN TIEGHEM, though the results incidentally mentioned by later investigators of more or less related problems suggest the desirability of an examination of the evidence for his conclusion. Such an examination convinced me that we do not know whether the passage of the lateral root through the cortex is accomplished merely by mechanical pressure, or by a digestion of the cortical tissue, or by a combination of such methods.

It was my good fortune to be able to investigate this problem during the winter of 1907–1908 under the direction of Professor LUDWIG JOST at Bonn and at Strassburg. I am also indebted to the New York Botanical Garden for courtesies extended during the preparation of the manuscript.

Literature

After an extended anatomical study of the origin and emergence of lateral roots, VAN TIEGHEM[2] concluded that the young lateral root emerges by the dissolution of intervening tissue, and that this dissolution is accomplished by enzymes. In the case of the vascular cryptogams the meristematic pericycle is the secreting tissue, and in the case of the phanerogams this function is performed by the meristematic endodermis. His conception is that the young lateral root digests its way through the cortex just as an embryo digests its endosperm. Why VAN TIEGHEM was led to this conclusion is not clear, as he does not offer any substantial evidence, and I have been unable

[1] From the botanical laboratory of the Kaiser Wilhelm University, Strassburg.

[2] VAN TIEGHEM, PH., Traité de botanique. Deuxième édition. pp. 709–711. Paris. 1891.

to find in the numerous figures of VAN TIEGHEM and DOULIOT[3] any trace of corrosion of cell walls or actual evidence of digestion. The figures do not show the stratum of compressed and collapsed cells which surrounds the young lateral root, at least in the cases of *Lupinus albus* and *Vicia Faba*.

Before VAN TIEGHEM, the same general conclusion as to the digestive action of the lateral root was expressed by REINKE.[4] The figures of REINKE are more accurate than VAN TIEGHEM'S, as in *pl. 2, figs. 5, 9*, the layer of distorted and collapsed cells which surrounds the young lateral root is shown. Still the figures do not show actual evidence of digestion.

Earlier than VAN TIEGHEM but later than REINKE, VONHÖNE[5] undertook to ascertain the relative importance of mechanical pressure and enzyme activity in the emergence of endogenous organs. His conclusion is (p. 230) that the young lateral root secretes a substance which acts upon the cortical tissue and digests it, just as does the enzyme secreted by the embryo of a seed digest its endosperm.

PFEFFER[6] (p. 367) notes that the passage of lateral roots through the cortex may be purely mechanical, though aided perhaps by some correlative activity on the part of the cortical tissue.

PEIRCE,[7] in his study of the penetration of living tissue by the roots of Vicia and Pisum, found that the root mechanically pushes its way through the various tissues tested. The results of CZAPEK[8] also support PEIRCE, since the former was unable to find any evidence of diastatic or of inverting ferments in the excretion of the

3 VAN TIEGHEM, PH., ET DOULIOT, H., Recherches comparatives sur l'origine des membres endogènes dans les plantes vasculaires. Ann. Sci. Nat. Bot. VII. **8**: 1–660. *pls. 1–40.* 1888.

4 REINKE, JOHANNES, Untersuchungen über Wachsthumsgeschichte und Morphologie der Phanerogamen-Wurzel. HANSTEIN'S Bot. Abhand. Gebiet Morphol. und Physiol. 13:1–38. 1871.

5 VONHÖNE, H. VON, Ueber das Hervorbrechen endogener Organe aus dem Mutterorgane. Flora **63**:227–234, 243–257, 268–274. 1880.

6 PFEFFER, W., Druck- und Arbeitleistung durch wachsende Pflanzen. Abhand. Königl. Sächs. Gesells. Wiss. **20**3:235–474. 1893.

7 PEIRCE, GEO. J., Das Eindringen von Wurzeln in lebendige Gewebe. Bot. Zeit. **52**:169–176. 1894.

8 CZAPEK, FRIEDRICH, Zur Lehre der Wurzelausscheidungen. Jahrb. Wiss. Bot. **29**:321–390. 1896.

roots of higher plants. PEIRCE'S conclusion is also supported by the results of OLUFSEN.[9]

Macroscopic study of the seedling

By examination of the seedlings of *Vicia Faba* one may find instances in which the cortex in the region of juncture of radicle and hypocotyl is strongly ruptured. In such cases one usually finds that two or more lateral roots have originated side by side, and their combined mechanical pressure has caused a rupture of the cortical tissue. The mere observation was made by VONHÖNE, but its significance apparently did not impress him. Evidently any digestion of the cortex that may occur is too slow to provide space for the advancing lateral root. Of course one cannot say positively that the fissure of the cortex is directly caused by the emerging lateral root. However, I have not found a rupture of the cortex except in association with lateral roots. Further, one may find swollen places on the radicle which are beyond doubt caused by the pressure of the advancing lateral root (*fig. 1*).

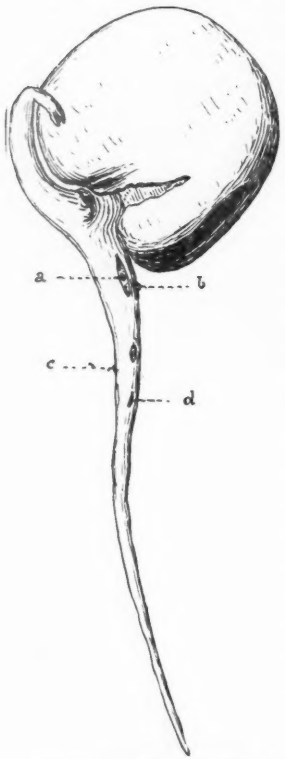


FIG. 1.—Seedling of *Vicia Faba: a*, rupture of cortex through which lateral root is emerging; *b*, c, cortex bulging because of pressure exerted by the lateral roots, which have not yet emerged; *d*, early rupture of cortex at point of emergence of lateral root.

Microscopic study of unemerged lateral root

All attempts to get microtome sections were unsuccessful, as the collapsed cells surrounding the young lateral root are lost in the preparation of the sections. All of my observations were

[9] OLUFSEN, LAURITS, Untersuchungen über Wundperidermbildung an Kartoffelknollen. Bot. Centralbl. Beih. 15:267–308. 1903.

made, therefore, from freehand sections mounted in pure lactic acid mixed with iodin. In order to have the sections clear and free from air, they were exhausted under the air pump. Only *Vicia Faba* and *Lupinus albus* were studied. Radial sections of the radicle showing the lateral root in median view are the best.

The cells of the cortex are not compressed to the stage of collapse until the lateral root has advanced about one-half the distance toward the epidermis. In earlier stages, when the lateral root has advanced only two-fifths the distance toward the cuticle, one may still find all the cells of the cortex uncollapsed and in natural cell connection, though of course displaced and compressed. The lateral root, therefore, has made a very difficult part of its journey without the slightest possibility of any digestion of the cortical cells. In the lupin the cells of the cortex have too little starch to note any possible autolysis, but in Vicia there is plenty of starch, and one can easily see that there is no difference in the starch content of the cells immediately surrounding the lateral root in comparison with those of other regions of the cortex. The same is true when the lateral root has advanced to the epidermis. Even in the cells which have been compressed to collapse, and in which the protoplasm looks wasted, the starch seems to be present in undiminished quantity. When the lateral root has advanced about one-half the distance toward the cuticle, the cell connection of the cells just outside the apex of the lateral root is broken in that region, and the cortical cells are thus pushed aside by the lateral root as is water by a boat. Those cells though now collapsed may remain undigested and be carried by the lateral root outside the epidermis. I have found, though very rarely, cases in which the cell connection of the displaced cortical cells was complete along the side of the lateral root, even at the time of the arrival of the latter at the epidermis. Any digestion of such cells is therefore excluded. Usually the cortical cells are so dislocated and so disarranged that the cell connection cannot be established. However, a few cases only are necessary to show that there can be no digestive action on the part of the lateral root either upon the cells of the cortex or of their contents.

Of course there must be some resorption of substance, and whether this is done by the cortex or by the lateral root I cannot say. As the

cortical cells collapse, the protoplasm of course loses its turgor and further compression drives the cell sap from the cell. Since the osmotic pressure of the lateral root is much higher than that of the cortical cells, there is probably some adjustment in the matter of resorption. Some of the solutes may go into the cortex and others into the lateral root. The apical cells of the lateral root are abundantly filled with starch, much more so than those of the cortex.

Turgor estimations

If the young lateral root mechanically pushes its way through the cortex, one would expect to find that the turgor of the cortical cells is less than that of the cells of the advancing lateral root. Longitudinal sections of the main root showing the lateral root in median view were immersed in various concentrations of potassium nitrate and of ammonium chlorid. After being exhausted under the air pump for thirty minutes, the degree of plasmolysis was determined. Essentially the same figures were obtained for *Vicia Faba* and for *Lupinus albus*. The figures given hold for sections in which the lateral root has nearly emerged. In 2 per cent. KNO_3 no plasmolysis could be observed in any of the tissues; in 3 per cent. KNO_3 there was initial plasmolysis of the cortical cells only. The turgor of the cells of the central cylinder and of those of the endodermis undisturbed by a lateral root seems to be a little higher than that of the cortical cells. In 4 per cent. KNO_3 the cortical cells are strongly plasmolysed, the endodermal cells covering the apex of the lateral root are not at all plasmolysed, the cells of the central cylinder and those of the undisturbed endodermis are somewhat though not strongly plasmolysed. In 5 per cent. KNO_3 there is total plasmolysis of all the cells except those of the lateral root itself and of the endodermal cells covering the apex of the lateral root. Some cells at the base of the lateral root show plasmolysis in 5 per cent. KNO_3. In 6 per cent. KNO_3 the endodermal cells covering the apex of the lateral root show initial plasmolysis. The maximum turgor for the endodermis is found in those cells which cover the apex of the young lateral root. From the apical cells toward the base of the lateral root the turgor of the endodermal cells seems to gradually decline, until only a short distance in longitudinal direction of the main root from the base of

the lateral root the turgor is the same as that of the undisturbed endodermis. The turgor of the cells of the central cylinder was also found to be 0.5 to 1 per cent. KNO_3 higher than that of the cells of the cortex. Similar estimates were made with ammonium chlorid, whose osmotic pressure is practically twice that of KNO_3, and it was found that one-half the concentration produced corresponding degrees of plasmolysis. In other sections in which the young lateral root is just beginning to dislocate the endodermis, the turgor of the endodermal cells is not so high, only about 4 per cent. KNO_3. It is thus apparent that as the very young lateral root commences to make new cells, the difference between the turgor of the cortical cells and that of the endodermal cells covering the apex of the lateral root increases until it amounts to about ten atmospheres before the lateral root ruptures the epidermis. *There can be no doubt that the tissue of the lateral root is capable of sustaining a growth push far greater than the cortex is capable of resisting.*

I was not able to observe plasmolysis in the meristematic cells at the apex of the lateral root inside the endodermis. It is quite likely that volume determinations would have revealed some shrinkage, but in saturated KNO_3 no separation of protoplasm from the cell wall was seen. It is possible that the protoplasm was suddenly killed. RHEINHARDT[10] found that the lateral roots of *Vicia Faba* will develop and grow in solutions of sufficient concentration to mortally plasmolyse the surrounding tissue.

The penetration of one living root by another

For the purpose of auxiliary evidence, several tests were made to ascertain whether one main or lateral root can penetrate another radicle. A seedling with radicle 6 or 7 cm in length was pinned to a sheet of cork through the cotyledons, and under the hypocotyl, 1 or 2 cm from the cotyledons, a small block of cork was placed to raise the hypocotyl. A root model of glass tubing was drawn out and vertically held upon the hypocotyl while gypsum was placed around the tube and the seedling. As soon as the gypsum was hard

[10] RHEINHARDT, M. O., Plasmolytische Studien zur Kenntniss des Wachstums der Zellmembranen. Sonderabdruck aus der Festschrift für Schwendener. pp. 41. *pl. 14.* Berlin. 1899.

the model was withdrawn, and into the canal was inserted the radicle of another seedling, so that the tip of the latter almost touched the horizontal hypocotyl (*fig. 2*). The inserted seedling was then almost entirely covered with gypsum, and when hard the preparation was placed in sawdust. The block of cork under the hypocotyl was of course withdrawn, and thus the side of the hypocotyl opposite the entering root was not covered with gypsum, and if the entering root penetrated the hypocotyl it could find exit unobstructed by gypsum.

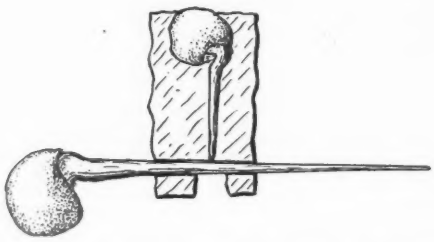


FIG. 2.—Arrangement of seedlings for penetration at right angles, the line-shaded portion representing solid gypsum.

Many such tests were made in which the main and lateral roots of *Vicia Faba*, *Lupinus albus*, and *Phaseolus multiflorus* were used in the various combinations, but the results were always negative. The preparations were allowed to stand undisturbed for various periods up to seven days, but the result was always negative. The radicle of the inserted seedling turned its tip as far as the canal would allow (less than the diameter of the radicle a mm. above the tip) and became imbedded in the callus subsequently formed. A strong imprint of the blunted radicle was always found on the hypocotyl, but microscopic examination showed the cuticle to be uncorroded and entirely intact. It is evident that if the radicle or the lateral root secretes an enzyme, such enzyme has no digestive action upon the cuticle. Apparently the mechanical push of the advancing root was not strong enough to break through the cuticle. However, no conclusion on this point is drawn here. It is significant, however, that in case the epidermis is ever so slightly wounded, as by piercing with a small glass point, either a main root or a lateral root will enter and pass entirely through the hypocotyl without formation of callus or other visible evidence of obstructed passage. Of course it is much easier to make an exit than an entrance through intact

cuticle if the latter is unwounded. When a root does enter, the passage is always around and not through the central cylinder, showing that the latter offers greater resistance than the cortex. Microscopic examination failed to reveal the slightest evidence of digestion of tissue. Many of the displaced cells of the cortex were found, but cells with broken walls were very scarce. The entering root apparently presses the cortical cells until they collapse, and then laterally displaces them without breaking the walls. No trace of corrosion of cell walls could be found. It seems probable that the mechanical push of the root is not sufficient to break through the cuticle when the latter is supported by underlying tissue. A demonstration for this, however, is not claimed.

Several tests were made to ascertain whether the central cylinder can be penetrated by another root at right angles. For this purpose enough cortex was removed to expose the stele, and the glass root model held so that when withdrawn from the gypsum the canal led directly to the central cylinder. In this way the entering root was compelled to enter the central cylinder at right angles or not at all. The result was negative in every case, and the entering root formed callus the same as in cases where the attempt was to enter the unwounded cuticle. The central cylinder was found to be strongly impressed, but no sign of corrosion or digestion of tissue could be observed. In some instances the entering root was able to shy from the stele and make passage through the cortex. Microscopic examination showed the cortex to contain compressed and collapsed cells. The appearance was the same as seen when the cortex is penetrated naturally by the lateral root. There was no evidence of corrosion, the walls of the collapsed cells being just as thick and regular in outline as those of the cortex in regions not affected by pressure.

Longitudinal passage through the stele by main and lateral roots

When the hypocotyl is traversed at right angles by another root, the tissue surrounding the path of the penetrating root cannot be examined microscopically with such advantage as is possible when the penetrating root traverses the hypocotyl longitudinally for a considerable distance.

The radicles of lupin seedlings having hypocotyls several centi-

meters long were amputated at the junction of stem and root. In the stele of the hypocotyl a vertical canal was made by inserting a small glass tube a few mm. and then withdrawing the tube. Into the canal was then inserted the root tip of a very young lupin seedling, and the whole preparation was then incased with gypsum and later placed in moist sawdust in vertical position (*fig. 3*). The parenchyma of the central cylinder offers the entering root the path of least resistance, so that the stele is often thus traversed its whole length. One may then make cross and longitudinal sections and very clearly study any changes in the tissues. As in the tests already described, no essential difference can be noted between the action of a main root and a lateral root on the tissues traversed by them.

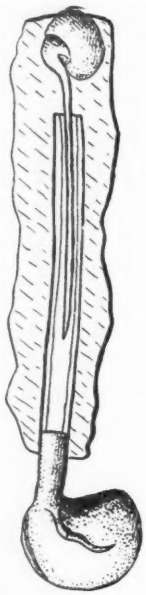


FIG. 3.—The radicle of the smaller seedling is growing downward through the central cylinder of the larger seedling's hypocotyl; the line-shaded portion represents solid gypsum.

The stele of the lupin is surrounded by a sheath which is only one cell in width, and the cells of this sheath only contain starch in any abundance. The cross-section thus stained with iodin shows the cylinder inclosed by a circle of starch-bearing cells. In cases in which the traversing root has pressed against this sheath, one may easily observe that even in cells of the sheath collapsed by the pressure the starch is present in undiminished quantity. There is no evidence of digestion of the starch either on the part of the entered root or by autolysis in the cells themselves. As one sections farther and farther along the hypocotyl, until only about 6 or 7^{mm} of the radicle remain within the hypocotyl, it may be observed, if the hypocotyl is allowed to remain undisturbed for a moment, that the radicle is gradually pressed out of the central cylinder, showing that it has encountered resistance from the tissues and that the latter recover from the pressure of the root. That the cells

of the central cylinder are under compression there can be no doubt, and that this compression provides some of the space occupied by the advancing root is also very clear. The collapse of some of the cells also provides space, and I am inclined to believe that in those two ways alone is the space occupied by the ingrowing root to be accounted for. Immediately surrounding the radicle, as seen in cross-section of the hypocotyl containing it, is to be found a stratum of collapsed cells which are so tightly compressed that one cannot count the individual cells. The walls are not corroded, however, and there is no evidence of wasting away of the tissue or of resorption of the cell walls. In some cells the protoplasm shows a little indication of wasting away, but it is too slight to count as a factor so far as the progress of the in-growing root is concerned. Beyond the cells which cannot be distinguished as separate units are those which can be so distinguished but which show compression without collapse. I have not in any case been able to account for each cell, but more than one-half the number can be found, which, together with those too much compressed to be distinguished, plus the space provided by compression, practically accounts for all the space occupied by the in-grown root. The compression is quite strong, as one may find cases in which the central cylinder is widely ruptured with the fissure extending for some distance into the cortex. Examination of the cells in immediate contact with the apex of the in-grown root shows them to be intact, so far as any corrosion or wasting-away of the walls is concerned.

Substitution of glass rod for the entering root

For the sake of greater certainty, preparations like the above were made except that a glass rod was vertically pushed into the central cylinder by a weight of from 300 to 400^{gm}. The rod was drawn out to resemble a root in form. After 48 hours under the weight the rod was removed and the tissues examined. The progress of the rod into the cylinder was somewhat slower than that of the growing root. The examination showed, however, no essential difference in the effect upon the tissues of the hypocotyl. One could not say from the microscopical examination whether the cylinder had been traversed by a root or by a glass rod. The compressed and collapsed cells had the same appearance as seen in other tests with root.

The passage of radicles and lateral roots through potato

Since PEIRCE found the penetration of living tissue by roots to be purely mechanical, I was not surprised at my failure to find sign of chemical activity on the part of penetrating roots in the tests above described. PEIRCE, however, found the radicle of Pisum able to enter the unwounded potato, a result which was difficult to understand, as I was inclined to assume the hypocotyl of Vicia and Lupinus to be more delicate than the epidermis or periderm of potato. A repetition of PEIRCE's experiment gave negative results. I tried both old and new potatoes, and also fitted glass tube tips to the advancing root to reduce deviation of the tip, but in each test the result was negative. Since PEIRCE used Pisum in his test, I tried that also, in addition to Lupinus and Vicia. If the periderm or epidermis is wounded, an easy entrance is effected by those radicles, and the root advances into the flesh of the potato. In tests with unwounded periderm there was always a deep impression of the potato. Microscopic examination showed that the periderm cells were compressed and to some extent the hypodermal tissue also, but there was no sign of corrosion. The advancing root formed callus, but when the periderm is wounded the callus does not form, and no evidence of obstructed passage is visible.

For the sake of another method a potato was cut into halves and the two halves tightly bound together with cord, so that the outside of one half was in contact with the outside of the other half. Perforations extending to within a few mm. of the periderm were made in one half, and into each perforation a seedling was inserted. The whole preparation was then incased with gypsum. Thus each radicle after penetrating a few mm. of the potato hypoderm found itself in contact with the inner side of the periderm. Further advance brought the tip of the radicle against the periderm of the other half of the potato from the outside. Strong impressions were made upon the periderm from outside. Microscopical examination showed no sign of any chemical activity. Since those same radicles readily traverse the flesh of the potato but do not enter the periderm from the outside, one is almost forced to the conclusion that the mechanical push is too weak. The advancing root simply follows the path of least resistance as long as an advance or deviation is possible. When

further advance is impossible, callus forms. Microscopical examination of the flesh of a potato through which a radicle has passed showed no evidence of any digestive action. The collapsed cells with uncorroded walls could be easily found, though the full number of cells required to occupy the volume of the tissue displaced by the radicle was not found in any given section. Compressed tissue too strongly compressed to allow a cell count was however present. No remnants of cells with frayed walls could be found. I did not see evidence of starch digestion in the immediate region through which the radicle passed. In many of the collapsed cells whose protoplasm appeared partially disintegrated, apparently intact starch grains were easily visible. There was no evidence of an active autolysis of starch grains in the cells.

Conclusion

The lateral roots of *Vicia Faba* and of *Lupinus albus* push out from the central cylinder through the cortex *mechanically* and do not have a digestive action upon the surrounding tissue.

New York City

STUDIES IN THE GRAMINEAE

IX. THE GRAMINEAE OF THE ALPINE REGION OF THE ROCKY MOUNTAINS IN COLORADO

THEO. HOLM

(WITH FIVE FIGURES AND PLATE XXX)

The object of the present paper is to offer a small contribution to the knowledge of the alpine vegetation of the Rocky Mountains, which I explored during the summers of 1896 and 1899. It is the intention especially to present some data in regard to the geographical distribution and to make a comparison between the grass vegetation of these mountains and that of mountains in the Old World; also that of the polar regions, which I had the opportunity to visit as a member of three Danish expeditions. Furthermore, I thought that a comparison of the alpine species with those from the wooded belts and the plains of Colorado might be of some interest; and finally a brief anatomical description of the alpine types has been inserted, since thus far the Gramineae have been much neglected in works dealing with structures of alpine plants. It will be seen that the geographical distribution of these species shows several points of interest, more so than their structure; nevertheless, to do full justice to the study of the anatomical characteristics of alpine plants, a consideration of all the families that are represented in these regions is necessary, even if the monocotyledons are of less importance on account of the frequent uniformity in their internal structure.

The exact number of alpine species in Colorado is of course not known; the wild country is very far from being well explored, and the literature is scanty. A very instructive paper was published by Parry,[1] however, who gives a long list of species from these regions, among which 56 species are said to be confined to the bald exposures above the timber line, while 86 others are also to be found at lower

[1] PARRY, C. C., The Rocky Mountain alpine region. Am. Ass. Adv. Sci. **18**: 248; see also PORTER and COULTER, Synopsis of the flora of Colorado. Washington. 1874; GRAY and HOOKER, The vegetation of the Rocky Mountain region. Bull. U. S. Geol. Survey **6**: No. 1. 1880.

elevations. According to this author 58 of these species occur also in the European and Asiatic mountains, or in high northern latitudes of both hemispheres. He enumerates 9 Gramineae. Among the 168 species of flowering plants I collected in this region only 17 belong to the Gramineae. The largest family is the Compositae with 25 species; then follow the Cyperaceae with 20, and then the Gramineae. Just above timberline the vegetation is luxuriant to the full extent of the word, and a number of very different plants abound in the willow-thickets along the mountain brooks; at higher elevations we may observe a rich vegetation on the slopes, especially near the snowbanks; but when we cross the bowlder fields we meet only with a very scant, often extremely poor, vegetation. Among the plants which were observed on the very summit of these mountains may be mentioned *Poa Lettermanni*, *Festuca ovina supina*, *Claytonia megarrhiza*, *Stellaria umbellata*, etc., but none of the Cyperaceae. It seems as if the Gramineae are able to thrive at very high elevations, judging from the various records of alpine plants in Europe and Asia, as will be shown later. It might be stated at the same time that some of these are among those that occur in the most northerly points; for instance, *Alopecurus alpinus* at 83° 4′, *Poa flexuosa* at 82° 50′, and *Festuca brevifolia* at 82° 27′.

In the accompanying Table (I) I have enumerated the alpine species of Gramineae, which I collected on the following mountains: Long's Peak, James' Peak, Pike's Peak, Mt. Elbert, Mt. Massive, Mt. Kelso, Gray's Peak, and along the headwaters of Clear Creek. To these may be added *Deschampsia calycina* Presl. from the summit of Gray's Peak, collected by B. H. SMITH; and *Poa Pattersoni* Vas. from mountains near Gray's Peak, collected by H. N. PATTERSON. The altitude where these alpine species occur lies between 3350 and 4300^{m}. *Agrostis canina* var., *A. varians*, *Avena Mortoniana*, *Poa flexuosa*, *P. gracillima*, *P. Fendleriana*, *P. Lettermanni*, *P. Pattersoni*, *P. alpina*, *Festuca ovina supina*, *Deschampsia calycina*, *Agropyrum Scribneri*, and *A. violaceum* are in Colorado confined to the alpine region. The remaining species, on the other hand, were also observed at lower elevations, from the aspen zone (about 2500^{m}) to the spruce zone (about 3100^{m}). *Phleum alpinum*, for instance, descends to the aspen zone on Long's Peak, where it is very frequent

in swamps; *Calamagrostis purpurascens* follows the creeks throughout the spruce zone on Long's Peak and the region of Clear Creek Canyon; *C. canadensis acuminata* is only exceptionally alpine, and thrives best in the swamps of the aspen zone; *Deschampsia caespitosa* is most frequent and typically developed in the swamps of the aspen zone,

TABLE I

Alpine Gramineae from Colorado	Long's Peak	James' Peak	Pike's Peak	Mt. Elbert	Mt. Massive	Mt. Kelso	Gray's Peak	Headwaters of Clear Creek
Phleum alpinum L.*	..	..	..	+	+	..	..	..
Agrostis varians Trin	+	+	..	..	..	..	..	..
A. canina L. var	..	..	..	..	+	..	..	..
Calamagrostis purpurascens R. Br	+	..	..	..	+	..	+	..
C. canadensis acuminata Vas	..	..	..	..	..	+	..	..
Deschampsia caespitosa Beauv	..	+	..	..	+	+	+	+
Trisetum subspicatum Beauv	..	+	..	+	+	+	..	..
Avena Mortoniana Scribn	..	+	..	..	..	..	..	..
Poa rupicola (Vas.) Nash	..	..	..	+	+	..	+	..
P. flexuosa Wahl	+	..	..	+	..	+	+	..
P. gracillima Vas	..	..	..	..	..	+	..	..
P. Fendleriana (Steud.)	..	+	..	+	..	..	+	..
P. alpina L	+	..	..	+	+	+	..	..
P. Lettermanni Vas	..	..	+	..	..	..	..	..
Festuca ovina L	+	+	..	+	+	+	..	..
F. ovina supina Hack	+	..	+	+	..	..	+	..
Agropyrum violaceum Lge	..	..	..	..	..	+	..	..
A. Scribneri Vas	+	+	..	+	..	..	+	..

* A + indicates the presence of the species, dots its absence.

but it is also very common near the snowbanks at high elevations; *Trisetum subspicatum* does not descend much farther than just to the timberline; *Poa rupicola* descends to the aspen zone on James' Peak and near Central City, but only seldom; *Festuca ovina* was collected in the aspen zone near Central City, and in the spruce zone on Mt. Massive and Long's Peak.

The distribution of these alpine species on the Pacific and Atlantic coasts is shown in Table II.

It will be seen from this list that of the 20 alpine species from Colorado 13 occur also on the Pacific coast, and 7 on the Atlantic, where they are either alpine or arctic, with the exception of *Deschampsia calycina*. Only 9 of these occur also in the Old World. Table III

shows their distribution in the polar regions, in the northern parts of Europe and Asia, but south of the arctic, and in the mountains farther south.

TABLE II

	Pacific	Atlantic
Phleum alpinum	+	+
Agrostis varians	+	..
Calamagrostis purpurascens	+	..
C. canadensis acuminata	+	+
Deschampsia caespitosa	+	+
D. calycina	+	..
Trisetum subspicatum	+	+
Poa flexuosa	+	+
P. gracillima	+	..
P. Fendleriana	+	..
P. alpina	+	+
P. Lettermanni	+	..
Festuca ovina supina	+	+

TABLE III

	Polar regions															
	Arctic America	Greenland	Spitzbergen	Finmark	Russia	Novaja Zemlja	Siberia	Iceland	Faeroe Islands	Great Britain	Alps and Pyrenees	Caucasus	Baikal and Altai Mts.	Himalaya	Asiatic coast of Bering Strait
Phleum alpinum	+	+	..	+	+	..	..	+	..	+	+	+	+	+	+
Calamagrostis purpurascens	+	+	..	..	..	..	..	..	..	..	..	..	..	..	..
Deschampsia caespitosa	..	..	..	..	+	..	+	+	+	+	+	+	+	+	..
Trisetum subspicatum	+	+	+	+	+	+	+	+	..	..	+	+	+	+	..
Poa flexuosa	+	+	+	+	+	+	+	+	+	+	..	..	+	+	+
P. alpina	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Festuca ovina	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
F. ovina supina	+	+	+	+	+	+	+	..	..	..	..	..	..	..	..
Agropyrum violaceum	+	+	..	+	..	..	+	..	..	..	..	..	..	..	..

Four of these are circumpolar: *Trisetum subspicatum, Poa flexuosa, P. alpina,* and *Festuca ovina,* also the var. *supina. Calamagrostis purpurascens* is the only one that is confined to this continent and Greenland; *Agropyrum violaceum* occurs in the arctic regions of both hemispheres, and var. *supina* of *Festuca ovina* is also an inhabitant of these high northern regions outside America. All the others extend to the mountains farther south, and five of these have even

reached the Himalayas. According to CHEESEMAN,[2] *Deschampsia caespitosa macrantha* Hack. and *Trisetum subspicatum* occur in New Zealand, and the latter has also been recorded from the antarctic regions. *Deschampsia caespitosa* is in Arctic America, Greenland, Novaja Zemlja, and Arctic Siberia, mostly represented by vars. *brevifolia* Trautv. and *borealis* Trautv. *Agrostis canina* occurs in Greenland and in several forms, but the variety which I collected in Colorado is not among these. Professor HACKEL, who has kindly examined my specimens of Agrostis, thinks that my alpine *A. canina* is nearest to var. *pusilla* Aschers. et Graebn.

Tables II and III thus demonstrate the fact that the alpine Gramineae in Colorado represent an assemblage of several very distinct geographical types: some that are endemic to this particular region; some that occur also on the Pacific and Atlantic coasts; some that have reached the polar regions in certain parts of both hemispheres; some that are circumpolar; and finally some that have become dispersed throughout the mountainous districts farther south in Europe and Asia. Of the 20 species enumerated from the mountains of Colorado, 7 are arctic-alpine types. *Deschampsia caespitosa* and *Festuca ovina* are quite frequent in these alpine and arctic regions, but their widest distribution is within the lowlands of the temperate zones of both hemispheres; hence they are not "arctic-alpine" in the strict sense of the word.

The tribes that are thus represented in this alpine region are AGROSTIDEAE (5 spp.), AVENEAE (4 spp.), FESTUCEAE (8 spp.), and HORDEAE (2 spp.). They are represented by genera that are really cosmopolitan, and from Table III we have seen that some of the species are widely distributed in both hemispheres. These data alone might suffice to illustrate the principal points in regard to composition and geographical distribution; but in order to make the illustration more complete, it seems necessary to extend our comparison to the grass vegetation in the timbered belts and on the plains below; also to the vegetation of alpine regions of other mountains.

Beginning with the species of the spruce zone, it has been stated that some of the alpine species are found among them, where they become associated with a few types characteristic of the zone; and

[2] CHEESEMAN, T. F., Manual of the New Zealand flora. 1906.

with some others which are common also to the aspen zone below. The following were observed only in the spruce zone: *Sporobolus brevicalyx* Scribn., *Calamagrostis Langsdorffii* (Link) Trin., *C. Scribneri* Beal, *Agrostis humilis* Vas., *Poa reflexa* Vas. and Scribn., and *Festuca ovina pseudo-ovina;* while *Poa pratensis* L. was also collected in the aspen zone.

If we continue the comparison, and examine the species that occur in the aspen zone, we meet with a larger number of species of the same tribes that were observed at higher elevations, and with them there also occur some of the Chlorideae. Peculiar to this zone are: *Stipa minor* Scribn., *Muehlenbergia comata* Benth., *M. gracilis* Trin. and the var. *breviaristata* Vas., *Alopecurus aristulatus* Michx., *Sporobolus depauperatus* (Torr.) Scribn., *Agrostis exarata* Trin., *Trisetum montanum* Vas., *Koeleria cristata* Pers., *Glyceria americana* (Torr.), *G. Holmii* Beal, *Poa annua* L., *P. nemoralis* L., *Festuca Thurberi* Vas., *Bromus breviaristatus* Thurb., *B. Richardsonis* Link, *Hordeum nodosum* L., *Elymus Sitanion* Schult., and *E. brevifolius* (Sm.). Besides these there are a few species which occur here, but which more properly belong to the plains, where they are more abundant and more typically developed. These are *Agrostis scabra* Willd., *Schedonnardus texanus* Steud., *Bouteloua oligostachya* Torr., and *Atropis airoides* (Nutt.). The number of species of Gramineae observed in the mountainous regions, from the aspen zone to the summits, averages about 50, among which the Chlorideae are rather scantily represented.

Descending to the plains, at an elevation of 1500^{m} about 40 species belonging to the same tribes are found; the Andropogoneae and Paniceae are added; and the Chlorideae abound. The following species are very frequent: *Panicum virgatum* L., *P. capillare* L., *Aristida fasciculata* Torr., *Stipa comata* Trin. and Rupr., *S. viridula* Trin., *Eriocoma cuspidata* Nutt., *Cenchrus tribuloides* L., *Sporobolus cryptandrus* Muehl., *S. asperifolius* Thurb., *S. airoides* Torr., *Calamovilfa longifolia* (Hook.) Hack., *Agrostis scabra* Willd., *A. intermedia* Scribn., *A. alba* L., *Schedonnardus texanus* Steud., *Bouteloua oligostachya* Torr., *B. racemosa* Lag., *Buchloë dactyloides* Engelm., *Munroa squarrosa* (Nutt.) Torr., *Distichlis spicata* (L.) Grne., *Atropis airoides* (Nutt.), *Poa Buckleyana* Nash, *Festuca tenella* Willd., *Agro-*

pyrum occidentale Scribn. vars. *mollis* and *vivipara*, *A. tenerum* Vas., *A. spicatum* Pursh, *Hordeum jubatum* L., and *Elymus canadensis* L. Some others are more scattered, for instance: *Andropogon furcatus* Muehl., *Echinochloa crus-galli* (L.) Beauv., *Muehlenbergia glomerata* Trin., *Lycurus phleoides* H. B. K., *Setaria glauca* L., *Bouteloua prostrata* Lag., *Diplachne fascicularis* (Lam.) Beauv., *Eragrostis major* Host., etc.

This grass vegetation in the wooded belts and on the plains consists mostly of American types, and the very few species that are also represented in the Old World are mostly introduced, for instance: *Echinochloa crus-galli*, *Digitaria glabra*, *Setaria glauca*, *Eragrostis major*, and *Agrostis alba*. *Calamagrostis Langsdorffii*, which I found in the spruce zone on Mt. Massive, occurs also in the mountains of New England, Canada, Alaska, south to California, and is also an inhabitant of Europe and Asia. *Poa annua*, *P. nemoralis*, *P. pratensis*, and *Koeleria cristata*, widely distributed species in the Old World, especially in the lowlands of the cold temperate zone, are also represented in the aspen zone. *P. nemoralis* is very common and varies according to the substratum, whether dry rocks or rich soil, in thickets, along streams, etc.

In comparing the geographical distribution of these various species of Gramineae which occur in the alpine region, in the wooded belts of the mountains, and on the plains, it is noticeable that the genera of the alpine flora are more cosmopolitan than those of the lower levels. None of the genera of the alpine Gramineae are endemic, and about one-half of the species occur also in the Old World (cf. Table III). On the other hand, the presence of arctic and circumpolar species is characteristic of the alpine flora, species which may be regarded as remnants of an old glacial vegetation that migrated from the far north; but those endemic in Colorado may have developed in the alpine regions of these very mountains.

Let us now examine the grass vegetation of the alpine region of the Alps of Switzerland, the Pyrenees, the mountains of Norway, the Caucasus, and the Himalayas. In these mountains the tribes that occur in Colorado are found, besides the Phalarideae, of which *Hierochloa laxa* Br. has been reported from the Himalayas (5000^{m}), and *Anthoxanthum odoratum* L. from Switzerland and the Caucasus.

In the Alps of Switzerland the tribe Festuceae is the best represented, according to HEER.[3] There are four species of Festuca (*F. ovina* L., *F. pumila* All., *F. pilosa* Hall. fil., and *F. Halleri* Vill.) and five of Poa (*P. alpina* L., *P. caesia* Sm., *P. laxa* Hnke., *P. minor* Gaud., and *P. annua* L.). *Koeleria hirsuta* Gaud., *Sesleria coerulea* L., and *S. disticha* Pers. also are present. Four Aveneae occur here (*Avena distichophylla* Vill., *A. versicolor* Vill., *Deschampsia caespitosa* Beauv., and *Trisetum subspicatum* Beauv.); two small species of Agrostis (*A. rupestris* All. and *A. alpina* Scop.) represent, with *Phleum alpinum* L., the Agrostideae; while *Nardus stricta* L. is the only member of Hordeae, observed so far, in these regions. Of these species *Sesleria disticha* and *Poa laxa* have been recorded from the highest elevation (3000^{m}).

In the Pyrenees[4] the genera are about the same, with the addition of *Holcus caespitosus* Boiss. (Aveneae), *Molinia coerulea* Moench., and *Nardurus Lachenalii* Godr. (Festuceae). The Festuceae are here also best represented, numbering 17 species, among which the following are known also from Switzerland: *Sesleria disticha, Festuca Halleri, F. pumila, Poa laxa, P. caesia, P. minor,* and *P. alpina.* Among the Agrostideae, *Agrostis rupestris* and *A. alpina* are here accompanied by three other species: *A. setacea* Curt., *A. nevadensis* Boiss., and *A. capillaris* L., while *Phleum alpinum* is only known from the subalpine region of these mountains. The Aveneae are represented by *Deschampsia flexuosa,* while *D. caespitosa* occurs only at lower elevations; also by *Avena albinervis* Boiss., *A. Scheuchzerii* All., *Holcus caespitosus* Boiss., *Trisetum flavescens* Beauv., *T. velutinum* Boiss., *T. glaciale* Boiss., and *T. Gaudinianum* Boiss., while *T. subspicatum* does not reach the alpine region in these mountains. The Hordeae are also here only represented by *Nardus stricta.*

In the mountains of Norway[5] the alpine Gramineae number only 8 species: *Phleum alpinum, Aira alpina* L., *Trisetum subspicatum, Catabrosa algida* Fr., *Poa laxa, P. stricta* Lindeb., *P. flexuosa* Wahl., and *P. alpina,* all of which extend to the arctic region.

3 HEER, O., Ueber die nivale Flora der Schweitz. 1883.

4 D. MARIANO DEL AMO Y MORA, Flora Fanerogámica de la Peninsula Iberica. Granada 1:2. 1871.

5 BLYTT, M. N., Norges Flora. Christiania. 1861.

According to MEYER[6] 22 Gramineae are alpine in the Caucasus. Of special interest are *Phleum alpinum*, *Avena versicolor*, *Deschampsia flexuosa*, *Trisetum flavescens*, *Poa alpina*, *Koeleria cristata*, and *Festuca ovina*. Besides these it is interesting to notice the occurrence of *Calamagrostis caucasica* Trin., *Briza media* L., *Poa altaica* Trin., *Colpodium Steveni* Trin., and *Hordeum pratense* Huds.

If we extend the comparison to the Himalayas,[7] we notice the presence of 5 alpine species which occur also in Colorado (cf. Table III); also the occurrence of genera that are not represented in the other mountains, namely Hierochloa, Stipa, Deyeuxia, Danthonia, and Elymus (*E. sibiricus* L.). The very considerable elevation of 5500^{m} is in these mountains reached by *Trisetum subspicatum*, *Poa hirtiglumis* Hook. f., and *Elymus sibiricus* L.; from between 4500 and 5100^{m} the following are recorded: *Hierchloa laxa* Br., *Agrostis inaequiglumis* Griseb., *Deyeuxia compacta* Munro, *D. nivicola* Hook. f., *D. pulchella* Hook. f., *Deschampsia caespitosa*, *Catabrosa sikkimensis* Stapf, *Poa alpina* L., *P. attenuata* Trin., *P. nemoralis* L., *P. flexuosa* Wahl., *P. tremula* Stapf, and *Festuca valesiaca* Schleich. Two species of Stipa (*S. concinna* Hook. and *S. mongolica* Turcz.) ascend to an elevation of 4000^{m}.

The Himalayas are thus much richer in alpine types than any of the other mountains, a fact that becomes still more manifest when we compare the representatives of the other families. Nevertheless, the alpine Gramineae of the Himalayas do not possess any type which from a biologic point of view deviates to any great extent from those of Colorado. For instance, Stipa and Elymus are really the only alpine genera in which the structure of spikelets is quite distinct from that of most of the others. It seems altogether as if the alpine Gramineae are remarkably uniform in habit, and in floral structure.

In speaking of Colorado especially, we have not in the alpine region a single type that may be compared with Buchloë, Munroa, Sporobolus, or Distichlis from the lowlands. The alpine representatives are perennial, except *Deschampsia calycina;* they are mostly

[6] MEYER, Verzeichniss der Pflanzen, welche im Caucasus etc., gefunden sind. St. Petersburg. 1831.

[7] HOOKER, J. D., Flora of British India. London. 1894. Vol. 6.

caespitose or sometimes stoloniferous, but with simple culms, and with an inflorescence (spicate or paniculate) of the usual composition. The empty glumes show no peculiar structure, and the flowering glume is either awned or awnless, and not in any way different from the usual structure among grasses in general. The average height of these alpine Gramineae is in some cases much less, in other cases about the same as that of lowland species of the same genera. *Poa Lettermanii*, the species of Agrostis, and *Festuca ovina* are mere dwarfs, but *Agropyrum Scribneri* reaches a height of 50^{cm}, even at an elevation of 4000^{m}. *Agropyrum violaceum* at the same altitude has culms about 40^{cm} high; and the culms of *Deschampsia caespitosa*, *Calamagrostis purpurascens*, and *Poa gracillima* reach about the same height. In habit the alpine Gramineae do not exhibit any characteristics which might indicate the extreme conditions under which they live. The same is the case with those grasses that occur in the arctic region, where we meet with several species that do not occur farther south, but the habit of these is of the same general kind. It is very different with the representatives of most of the dicotyledonous families from the alpine and arctic regions; in these the habit is frequently so peculiar and characteristic that they are readily recognized as being either alpine or arctic. In other words, the monocotyledons, at least the Glumiflorae, do not appear to be influenced to any great extent by climate and soil, as are most of the dicotyledons, at least not in regard to their general habit in alpine or arctic regions.

An examination of the internal structure of these alpine species from Colorado will demonstrate probable characteristics in structure; "probable," because I am not in a position to make any comparison with species from other alpine regions. It is my intention merely to present these anatomical data for future comparison, when someone may feel induced to investigate the grass vegetation of other mountains, and especially from high altitudes. I have examined roots, culms, and leaves. The leaf structure might have been sufficient, and, as already stated, most authors have so far confined their work to the leaves alone. However, it does not appear to me that the structure of culms and roots should be neglected altogether, and especially not when dealing with plants that are able to persist under such extreme conditions.

The roots

In considering the internal structure of roots that are simply nutritive and of no long duration (perhaps only one season), we must not expect to find great modifications. In regard to the Gramineae we have learned from KLINGE'S[8] interesting paper that certain modifications may be observed in the structure of the cortex, whether persisting or collapsing, whether homogeneous or differentiated as distinct zones of parenchymatic or stereomatic strata; also in the thickening of the endodermis, and in the structure of the pericambium, whether it is continuous or interrupted by the proto-hadrome. The presence or absence of an exodermis also seems to be worth mention, and the structure of the parenchyma in the stele, which sometimes represents a central pith. Much attention has been given to the position of the proto-hadrome vessels, whether they are inside the pericambium or border directly on the endodermis. In some instances all these vessels have been observed to occupy the same position in reference to the pericambium; but in other instances a variation has been noticed, where only some of the proto-hadrome vessels had broken through the pericambium. In studying root structures of different plants, especially of monocotyledons, one gets the impression that the continuity or interruption of the pericambium is of some importance and constitutes a good anatomical character. In very many roots I have found a constantly continuous pericambium or a constantly interrupted one; but on the other hand, as shown in Eriocaulon and Carex,[9] there are also cases where this structure is not constant, but varies from the base to the apex of the same root. This peculiarity I noticed by making consecutive sections of a number of roots, and it appears therefore as if the structure of the pericambium, so far as concerns its continuity or interruption, is not a character to be depended upon. In *Deschampsia caespitosa* and *Festuca ovina* from Europe, KLINGE (*l. c.*, p. 56) observed the proto-hadrome vessels bordering on the endodermis; while in these same species from Colorado all the vessels were found to be inside the pericam-

[8] KLINGE, Vergleichend histiologische Untersuchung der Gramineen- und Cyperaceen-Wurzeln insbesondere der Wurzel-Leitbündel. Mém. Acad. Imp. St. Petersbourg VII. **26**: No. 12. 1879.

[9] BOT. GAZETTE **31**: 17. 1901; and Am. Journ. Sci. **10**: 278. 1900.

bium. Such discrepancies often occur, but they are hardly of any importance.

In the alpine Gramineae from Colorado the root structure is very uniform. The epidermis is hairy in all the species; a thin-walled exodermis was observed only in *Agropyrum violaceum*. The cortical parenchyma is mostly thin-walled and solid, but a radial collapsing was noticed in the species of Poa, with the exception of *P. alpina*, in Trisetum, and in Deschampsia. In the species of Agropyrum the peripheral strata of the cortex are stereomatic, and persistent in comparison with the inner, which are thin-walled and collapsed. The endodermis is generally thick-walled (*figs. 1–5, End*), representing a typical U-endodermis, or an O-endodermis, as was observed in specimens of *Poa alpina* from bowlder fields. The pericambium was found to be continuous in all the species, and it is generally thin-walled; but in the species of Agrostis (*fig. 2*), Calamagrostis, Trisetum, and in *Poa gracillima* it is more or less thick-walled. It consists mostly of a single layer, but in the species of Agropyrum (*fig. 5*) and Avena two or three layers are developed outside the proto-hadrome vessels. The number of hadromatic rays is of course very variable; in the thick roots of Trisetum, Deschampsia, Calamagrostis, Avena, and Agropyrum there may be as many as fifteen rays, but with mostly a single proto-hadrome vessel in each ray. In the species of Agrostis and Festuca the hadrome extends to the center of the stele, while in the others a central pith is developed. This pith is quite broad, and often conspicuously thick-walled, as in Trisetum, Agropyrum, Avena, and Calamagrostis.

It is interesting to note that in some cases the root structure corresponds with the nature of the substratum. For instance, in *Poa Lettermanni*, which I found growing in wet moss near the snowbanks, the root structure resembles that of a hydrophilous plant, with open cortex, thick-walled endodermis, and thin-walled pericambium. In the species of Agropyrum from very dry, stony soil, the peripheral strata of the cortex are stereomatic. In *Calamagrostis purpurascens* from similar stations there is a very compact cortex, a heavily thickened endodermis, a thick-walled pericambium, and a broad central, very thick-walled pith. A similar, very solid structure is also characteristic of the species of Festuca and

Agrostis, inhabitants of dry soil among bowlders. The roots of these species thus show in general the structure of xerophytes. But in *Poa alpina* no such distinction seems feasible, since the structure is identical whether the specimens are from wet soil in thickets of willows along mountain brooks, or from dry soil among bowlders.

The culm

In describing the structure of the culm, attention must be given to the distribution of the mechanical tissue (stereome), to the minor structure and disposition of the mestome strands, and finally to the structure of the cortical parenchyma. In the character of the stereome our alpine Gramineae represent the type in which a circular band of this tissue (in cross-sections) is in contact with all the mestome bundles; it is the eleventh type of SCHWENDENER[10] and is the one most frequently observed in the Gramineae. While the principal feature of this type is that all the mestome strands are in contact with the mechanical tissue, some modifications are to be observed in regard to the relative development or strength of the stereome, especially in cases where the mestome bundles occur in different sizes, and in more than one circular band. Five very distinct modifications were observed in our alpine species, which may be readily distinguished by the accompanying figures, which I have drawn in a schematic way. The black represents the stereome; the peripheral white zone the cortex; the central white zone the pith; the orbicular and oval rings the mestome strands.

In these figures, *A* represents the most simple structure, where there are only five mestome strands, all the same size and outline (oval), and all imbedded in the stereome, which extends to epidermis, thus forming a strong, hypodermal support outside the leptome (*Agrostis canina*, var.). In *B* there are four large, oval mestome strands, alternating with four much smaller ones, which are orbicular in transverse section, and they are all surrounded by stereome, which only extends to the epidermis outside the larger ones (*Poa Lettermanni*, *P. alpina* from Long's Peak, and *Agrostis varians*). In *C* (*Poa rupicola*) there is also one band of mestome bundles, composed of

[10] SCHWENDENER, Das mechanische Princip im anatomischen Bau der Monocotylen 60. Leipzig. 1874.

larger (oval) and smaller (orbicular) ones; and hypodermal stereome occurs outside each of the mestome strands, but is only in contact with the leptome side of the larger ones; the smaller strands only touch the inner stereome with their hadrome side. When two concentric bands of mestome bundles occur, the peripheral ones are the smallest and are orbicular in cross-section; the inner ones are either

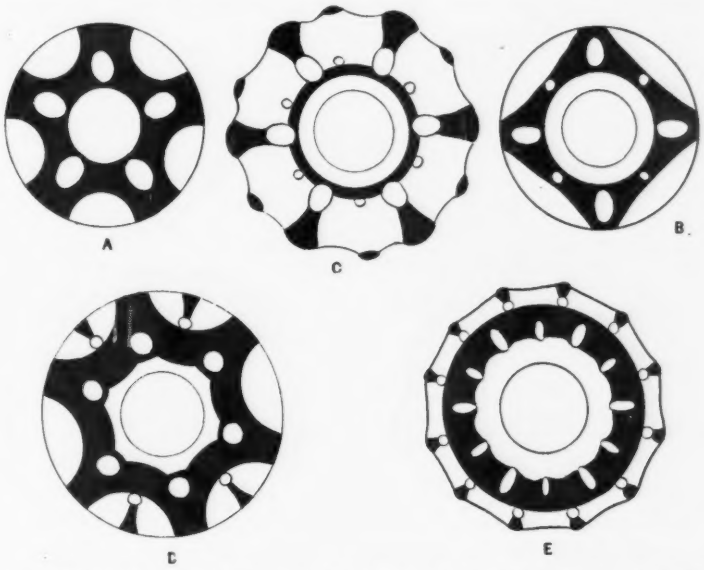


Diagram showing the structure of the culms of *Agrostis canina* var. (*A*), *Poa Lettermanni* (*B*), *P. rupicola* (*C*), *P. alpina* (*D*), and *Agropyrum violaceum* (*E*).

orbicular (*D*) or oval, often representing two sizes, as shown in *E*. In these culms (*D* and *E*) the stereome shows two well-marked modifications. It constitutes a mechanical support on the leptome side of all the mestome strands in *D;* while in *E* this hypodermal support is confined to the peripheral strands alone—those of the inner band (*E*) are imbedded in a zone of stereome, which does not extend to epidermis. The structure illustrated by *E* was observed in *Calamagrostis purpurascens*, *Agropyrum violaceum*, and *Deschampsia caespitosa* from Graymont; while *D* is the most frequent

structure exhibited by the remaining species, including *Poa alpina* from Mt. Kelso and *Deschampsia caespitosa* from Gray's Peak. These culms thus represent five types as to the occurrence of one or two bands of mestome bundles, and as to the distribution of the stereome as a circular band extending to the epidermis as hypodermal groups in contact with or separated from some of the mestome bundles (the latter case is illustrated in *C*).

The fact that two of these types (*D* and *E*) have been observed in one species (*Deschampsia caespitosa*), though from different elevations, seems to indicate that the structure may not be constant. The type *D* appears to be the most frequent in the alpine species of Colorado, and the most important difference between this and the three preceding (*A*, *B*, and *C*) depends upon the presence of two concentric bands of mestome bundles, all of which are supported by hypodermal stereome. The type *E* is more complicated on account of the inner mestome strands being of different size and lacking the hypodermal stereome, and this type, as stated above, was observed in *Agropyrum violaceum*. If this structure be compared with that of the French species of Agropyrum described by DUVAL-JOUVE, it is observed that it does not agree with any of them. The species examined by this author were lowland species, and several were maritime. Characteristic of these species is the occurrence of hypodermal stereome outside the smaller as well as the larger mestome strands; also in some species the inner band may be located nearer the center of the culm, a considerable distance from the stereomatic zone. In other words, the lowland species of Agropyrum in France represent actually an entirely distinct type of structure, which corresponds with the twelfth type of SCHWENDENER (*l. c.*), in which the inner mestome strands are in the pith, some distance from the stereomatic cylinder.

The minor structure of the mestome strands in our alpine species agrees in most respects with that of other Gramineae. It has been shown that some variation occurs in the outline of cross-sections, some being orbicular (especially the smaller ones), and the larger ones usually oval. The leptome and hadrome differ in no way from that of other species from lower elevations. A more or less thick-

[11] DUVAL-JOUVE, Etude anatomique de quelques Graminées et en particulier des Agropyrum de l'Hérault. Mém. Acad. Sci. Montpellier. Paris. 1870.

walled mestome sheath was observed in all the alpine Gramineae, and these species may thus be added to the list given by SCHWENDENER[12] in his paper on mestome sheaths. However, the presence or absence of the mestome sheath, as already pointed out by SCHWENDENER (*l. c.*, p. 415), is merely of taxonomic importance. This may be readily seen from his list, according to which this sheath is not developed in any of the species of Andropogoneae and Maydeae, or in certain genera of the Paniceae (Paspalum, Pennisetum, and Setaria). The fact that it occurs in some species of Panicum (*P. miliaceum*, *P. capillare*, *P. proliferum*), but not in others (*P. sanguinale*, *P. plicatum*, *P. colonum*, etc.), seems to indicate that these species represent very distinct types within the genus, as shown also by the external structure of their spikelets. The same conclusion may be drawn from the fact that the species of Aristida in which I observed a double parenchyma sheath,[13] but no mestome sheath, differ in a marked degree from those which possess this sheath, and in which only a single parenchyma sheath is developed; we have here to deal with a taxonomic, and not with an epharmonic character. By studying the anatomy of a number of Gramineae allied to or associated with Aristida, I found a mestome sheath constantly developed, whether the material was collected on the plains, the prairies, in woodlands, or in marshes. If on the other hand the structure of the mestome sheath is examined, some kind of modification in the thickening of the cell walls is noticed, which evidently constitutes an epharmonic character; in the alpine species this sheath was generally observed to be quite thick-walled. The presence or absence of thick-walled mestome parenchyma as a stratum between the leptome and the hadrome is to be considered only of taxonomic importance; such parenchyma was not observed in *Poa Lettermanni*, *P. gracillima*, *P. rupicola*, or in the species of Festuca and Avena, but in all the others.

Of much greater interest, however, is the structure of the cortical parenchyma. This tissue is very compact in these Gramineae with the exception only of *Poa Fendleriana*, *P. gracillima*, and *Phleum alpinum*. It is either developed as a palisade tissue of several layers

[12] SCHWENDENER, Die Mestomscheiden der Gramineenblätter. Sitgungsber. Berliner Akad. Wiss. 413. 1890.

[13] HOLM, THEO. Some new anatomical characters for certain Gramineae. Beih. Bot. Centralbl. 11:—. 1901.

(*fig. 6, C*) or as a homogeneous tissue of roundish cells (in cross-section). The former structure is the most frequent, and especially well represented in *Poa rupicola*, *P. Lettermanni* (*fig. 6*), and *Agrostis canina;* the latter structure was observed in *Agrostis varians*, *Poa flexuosa*, Agropyrum, Calamagrostis, Deschampsia, and Festuca.

We will finally consider the structure of the cuticle and epidermis. The cuticle was observed to be smooth and quite thick in all the species, even in the densely hairy Trisetum. The epidermis is scabrous in Calamagrostis, hairy in Trisetum, but glabrous in the others. Some slight variation in the structure of the cell walls was noticed; the outer wall, for instance, is quite thick as compared with the inner and the radial, and this structure seems to be the most frequent. But in *Agrostis canina*, *Poa rupicola*, *Phleum alpinum*, and *Agropyrum violaceum* all the cell walls of epidermis were equally and quite heavily thickened.

A very firm structure is thus exhibited by the culms of our alpine Gramineae, so far as concerns the mechanical tissue and the dense cortical parenchyma covered by a thick-walled epidermis. It is also interesting to notice that the cortex generally contains much chlorophyll, and that the cells are developed as typical palisades, thus being able to perform the function of the chlorenchyma in the leaves. The modifications in structure in the culms depend mostly upon the distribution of the stereome, and upon the mestome strands (their relative size, their mechanical support, and their disposition in one or two concentric bands). The pith, on the other hand, shows no deviation from the most common structure known in this family; it was constantly found to be thin-walled and broken in the center, and with no deposits of starch.

The leaves

In the leaves the epidermis and chlorenchyma offer some distinctions of importance, and much more so than the stereome, at least in the alpine species. However, the structure is very uniform, and does not exhibit any such prominent epharmonic characters as are so well known from species of the lowlands, the plains, and the prairies. In the alpine species the leaf structure is very firm throughout; there are no wide intercellular spaces in the chlorenchyma, and no water-

storage tissue surrounding the veins. The distribution of the stereome is mainly the same in all the species and rather scantily represented as compared with the culm. The mestome strands are constantly arranged in a single plane and are very uniform in structure.

In the epidermis the outer cell wall is generally quite thick on the dorsal face, but less so on the ventral; the cuticle is smooth, and very distinct in all the species. The characteristic bulliform cells between the mestome strands on the upper face of the blade were observed in all the species, but they are not very large, and are sometimes confined to a single group, one on each side of the midrib, as in *Poa Lettermanni*, *P. flexuosa*, *P. gracillima*, and *P. rupicola*; in the other species there may be four to six or even a larger number of groups in the lateral parts of the leaf blade. In *Poa Lettermanni* (*figs. 7, 8*) the leaves are glabrous on both faces, but in the other species they are generally a little scabrous from small, obtuse papillae. Pointed, prickle-like projections occur in Festuca, Agrostis, *Poa rupicola*, *P. Fendleriana*, and *P. alpina* from Long's Peak. Hairs are not frequent, but were observed on the ventral face of the blade in *Poa gracillima*, Calamagrostis, and Avena, and on both faces in Trisetum and *Agropyrum Scribneri*. With the exception of *Trisetum subspicatum*, which may be called densely hairy, the hairs in the other Gramineae are so scattered that they are often hardly visible to the naked eye.

The stomata (*fig. 7*) occur mostly on both faces of the blade, but as a rule are most frequent on the ventral face; in some species of Poa, *Agropyrum Scribneri*, Calamagrostis, and Trisetum they are confined to the ventral face. They are usually sunk, and sometimes covered by papillae or hairs, and they occur especially on the sides of the furrows between the mestome bundles. Their position in reference to the surface may sometimes vary on the same leaf; for instance, in *Agropyrum violaceum* they are free on the ventral face, but sunk on the dorsal, while the opposite is true of Avena; in *Deschampsia caespitosa* they are level with the epidermis, and not covered by the papillae. Otherwise the structure of the epidermis offers no points of particular interest.

The stereome is poorly represented in most of these species, and occurs often only as a very small hypodermal strand outside the larger mestome bundles (*fig. 8*) and not in contact with them; it is better

developed in the margins of the leaves. The mestome strands show the same structure in regard to the leptome and hadrome as observed in the culm; there is also the same variation from oval to orbicular (in cross-section), and the mestome sheath is typically developed with the inner cell wall heavily thickened. Outside the mestome sheath the ordinary thin-walled parenchyma sheath is found mostly containing some chlorophyll. I have not observed a single instance in these alpine species where mestome strands occurred beneath the bulliform cells; but in *Deschampsia caespitosa* from Graymont, at a much lower elevation, some few very fine veins were observed between the larger ones, thus being located directly underneath the bulliform cells. It might be mentioned at the same time that DUVAL-JOUVE (*l. c., pl. 16, fig. 5*) figures a leaf of a French specimen in which a very small mestome strand occurs between each of the two larger veins, just beneath the bulliform cells.

The chlorenchyma is very compact in these alpine species, and is mostly developed as a palisade tissue. In *Poa Lettermanni*, however, it is developed as palisades only around the mestome strands, radiating toward their center, while in the other portions of the leaf this tissue consists of much shorter and roundish cells (*figs. 7, 8*). In *Poa flexuosa* there are no palisades at all; in Phleum the cells are hardly high enough to be called palisades, even if some distinction may be noticed between the ventral and dorsal portion of the chlorenchyma. In all the other species the chlorenchyma constitutes a homogeneous palisade tissue, vertical to the surface or radiating toward the center of the mestome bundles. It is a very compact tissue throughout the leaf blade, and rich in chlorophyll.

The leaves of the alpine Gramineae are mostly erect, though not exactly vertical, and are frequently conduplicate or with the margins involute; they are seldom spreading or perfectly flat. In this way they agree to some extent with the species from the plains, although the internal structure is very different, at least in certain genera. In the alpine species the leaves are often furrowed on the ventral face, but not to the extent so commonly observed in the lowland species, in those that inhabit the plains for instance. This may perhaps be the reason why the stomata in the alpine species are so much deeper than in those from the lowlands, where they are level with the epidermis, but

protected by the more ample covering of papillae or hairs, and also by the greater depth of the furrows. In the leaves of the lowland species the stereome is better represented, the bulliform cells generally larger, and frequently accompanied by several strata of a colorless tissue, the so-called water-storage tissue, which is not developed in the alpine species. But in the chlorenchyma of the Gramineae from the plains and prairies we find a more or less homogeneous tissue of palisades occupying the position described above. Finally the fact must be mentioned that the stomata being most frequent on the ventral face of the leaf is a feature the alpine Gramineae have in common with nearly all those which I have examined from the lowlands, and especially those from the plains and prairies, with the exception of Sporobolus, Munroa, and Calamovilfa. In the woodland types of Muehlenbergia the stomata are almost equally distributed on both faces of the leaf blade; while in the species of the same genus from dry, rocky mountain slopes, the stomata are confined to the ventral face and protected by the folding of the blade. In species from wet soil, meadows, or swamps, the stomata are most frequent on the dorsal face in Leersia; while in Amphicarpum from moist pine barrens they are distributed over both faces, though most numerous on the ventral; in *Uniola latifolia* from shaded slopes the stomata occur only on the ventral face, and this same disposition is to be found also in *Pleuropogon Sabinei* from arctic swamps. DUVAL-JOUVE, who has examined a large number of Gramineae,[14] speaks of the difficulty of giving any precise information about the distribution of stomata in this family. He observed also that the ventral face of the blade is sometimes the only one where the stomata occur, but at the same time he noticed that a torsion of the leaf took place, thus exposing the dorsal face to the sun instead of the ventral. In this way the stomata become well protected, but in our alpine types the only protection seems to depend upon the folding of the blade, conduplicate or with the margins involute.

The leaf structure of alpine plants has been described and explained by several authors, but the Gramineae have been neglected, and evidently because the narrow leaves appear to be more uniform in

[14] DUVAL-JOUVE, Histotaxie des feuilles de Graminées. Ann. Sci. Nat. Bot. VI. 1:314.

structure and apparently of less interest. I am not in the position to draw any anatomical comparison, therefore, between the species from the Rocky Mountains and those from other alpine regions. The alpine types which have been treated and studied in Europe are nearly all dicotyledons, and the results are not quite comparable to those derived from the study of our Gramineae. According to BONNIER[15] and WAGNER,[16] the palisade tissue should be far better developed in the alpine forms (dicotyledons) than in those from the lowlands; the leaves should be thicker, and the structure more open on account of the wider intercellular spaces; also the alpine leaves should be more thoroughly dorsiventral, with stomata sometimes more abundant on the ventral than on the dorsal face; the guard cells should be level with the epidermis except in species with evergreen leaves (Ericaceae, etc.).

These distinctions are not to be observed in the Gramineae. We have seen that in the alpine representatives of this family the leaves are not dorsiventral; the palisade tissue is not developed to any greater extent than in the lowland species; the chlorenchyma is not open, on the contrary it is very compact; also the stomata are not level with the epidermis but mostly sunken. It seems almost safe to conclude that the epharmonic characters are much less pronounced in the alpine Gramineae than in the dicotyledons from similar high situations, when compared with the corresponding lowland types. Much would be learned, however, by examining alpine Gramineae from other parts of the world, and especially other genera and species than those described in the preceding pages. Also the study of alpine types ought not to be restricted to a mere consideration of the foliar organs, even if these unquestionably are the most important; the structure of stem and root ought not to be excluded altogether, as is frequently or nearly always the case.

Conclusions

We have seen that the alpine Gramineae of Colorado constitute an assemblage of very distinct geographical types; some that are only

[15] BONNIER, GASTON, Cultures expérimentales dans les hautes altitudes. Compt. Rend. Acad. Sci. 1890; Etude expérimentale sur l'influence du climat alpin sur la végétation et les fonctions des plantes. Bull. Soc. Bot. France **1888**: 436.

[16] WAGNER, Zur Kenntniss des Blattbaues der Alpenpflanzen und dessen biologischer Bedeutung. Sitgungsber. K. Akad. Wiss. Wien **101**: 59. 1892.

known from the alpine regions of this country; others that are known also from the higher mountains of Eurasia; some that have reached the polar regions, among which several are circumpolar; and finally some that occur also at lower altitudes in these same mountains. The alpine genera seem to be more cosmopolitan than those observed at lower levels; as a matter of fact none of these genera of Gramineae are endemic to this country, and none of the alpine genera of Europe and Asia are endemic to those countries.

The habit and floral structures of the alpine Gramineae of Colorado are remarkably uniform and simple, when compared with some of the other species and genera from the lowlands. Corresponding with this uniformity in habit, we meet with no extraordinary development of any of the tissues. The anatomical structure is rather simple, and neither the stereome, nor the chlorenchyma, nor the stomata exhibit any feature that might be looked upon as characteristic of an alpine type. In this respect the alpine Gramineae differ from most of the other families, not so much, however, from the Cyperaceae as from the Juncaceae (Luzula and Juncus), and especially from the dicotyledons. The habit and internal structure of the alpine dicotyledons of Colorado are very distinct from those of their representatives which thrive at lower elevations in mountains or on the plains and prairies; very prominent distinctions of this kind I have observed in a number of alpine genera, as Ranunculus, Trifolium, Claytonia, Stellaria, Synthyris, Mertensia, Primula, etc. Whatever conclusions may be drawn from the various treatments of alpine plants in general, and especially in regard to "adaptations," it must be borne in mind that the monocotyledons have so far been almost entirely ignored, although they are certainly of no small interest on account of their frequent occurrence and very wide distribution in the high alpine regions. It seems thus very unsafe to describe the alpine leaf "in general" without including the Gramineae, and for this purpose the present paper may be of some interest to future students of "alpine structures."

Brookland, D. C.

EXPLANATION OF PLATE XXX

Fig. 1.—Cross-section of root stele of *Poa Lettermanni: End*, endodermis; *P*, pericambium; *PL*, proto-leptome; *PH*, proto-hadrome. ×560.

FIG. 2.—Root stele of *Agrostis canina* var.; letters as above. ×560.

FIG. 3.—Root stele of *Festuca ovina;* letters as above. ×560.

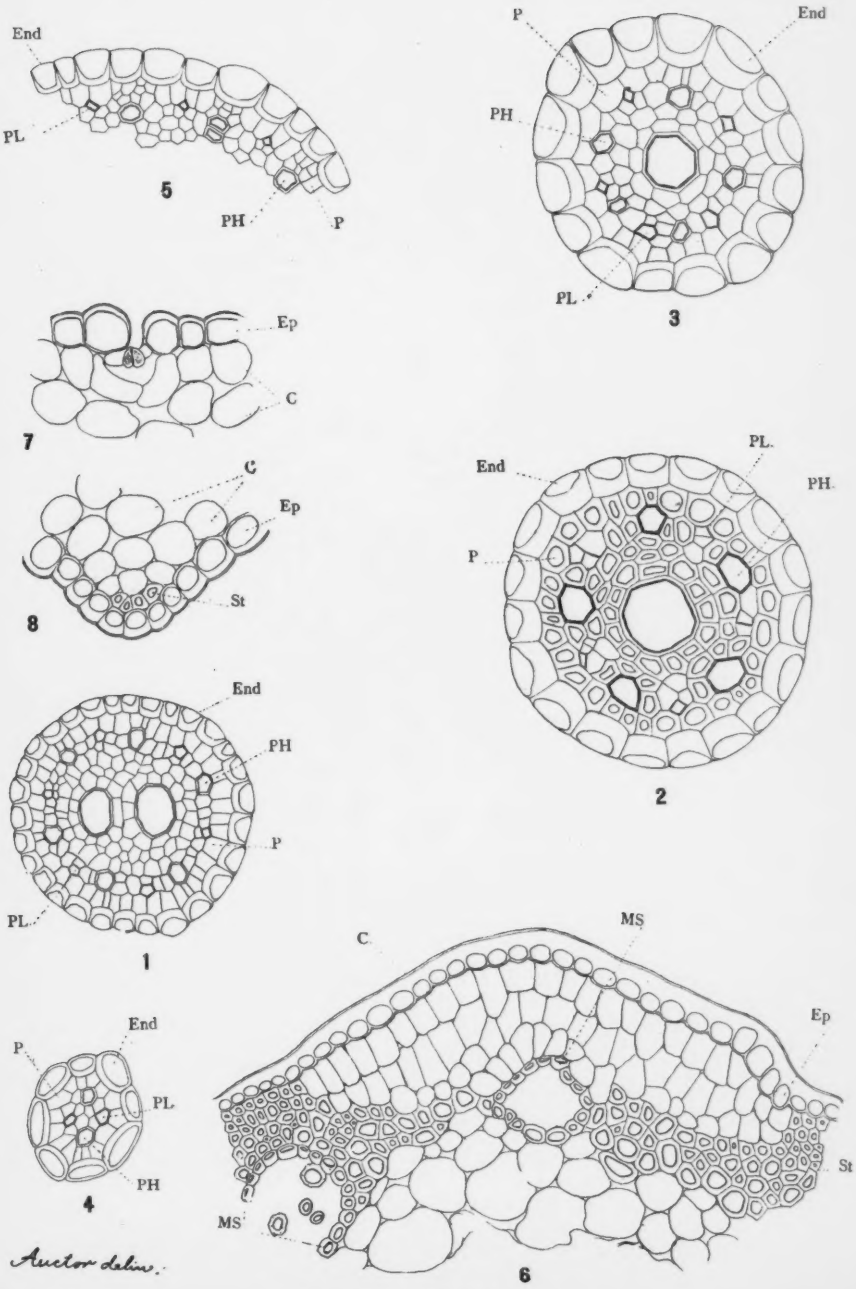
FIG. 4.—Root stele of *Poa flexuosa;* letters as above. ×560.

FIG. 5.—Part of root stele of *Agropyrum Scribneri;* letters as above. ×560.

FIG. 6.—Cross-section of part of culm of *Poa Lettermanni*, showing epidermis (*Ep*), cortex (*C*), stereome (*St*), and two mestome strands with their mestome sheaths (*MS*). ×400.

FIG. 7.—Same species; cross-section of leaf, showing ventral epidermis (*Ep*) with a stoma, and two strata of chlorenchyma (*C*). ×400.

FIG. 8.—Same species; cross-section of leaf, showing dorsal epidermis (*Ep*), hypodermal stereome (*St*), and chlorenchyma (*Ca*). ×400.



HOLM on ALPINE GRAMINEAE

THE NATURE OF THE EMBRYO SAC OF PEPEROMIA[1]

WILLIAM H. BROWN

(WITH PLATES XXXI–XXXIII)

At the suggestion of Professor DUNCAN S. JOHNSON, I undertook the cytological study of the development of the embryo sac of several species of Peperomia, with the purpose of finding out whether the development of this genus offered any support to the idea, recently advanced by several investigators, that when a row of megaspores is not formed, each of the first four nuclei of the embryo sac is to be regarded as a megaspore nucleus. The results found were exceptional and may be of interest, as they seem to throw some light on this question and also on the nature of the embryo sac of Peperomia.

For the investigation, Professor JOHNSON turned over to me material of three species which he had collected for this purpose. Material of *P. arifolia* was collected in the greenhouses in Baltimore. The material was fixed in chrom-acetic or Fleming's solutions. The sections were cut 10 μ thick and stained with Fleming's triple or Haidenhain's iron-alum hematoxylin. The latter stain was used alone or counterstained with gentian-violet or eosin.

This paper does not pretend to be a study of the whole life-history of Peperomia, but deals in detail only with the development of the embryo sac. It is hoped, however, that this will throw some light on the origin of the peculiarities which have been described in its later development.

The sixteen-nucleate embryo sac of Peperomia was discovered in *Peperomia pellucida* by CAMPBELL ('99), who, however, misinterpreted some of its features. JOHNSON ('00) describes the mature sac of *P. pellucida* as containing one egg, one cell with the position of a synergid, six nuclei which are cut off singly against the wall of the sac and finally degenerate, and eight which fuse to form the endosperm nucleus. The archesporium consists of a single hypodermal cell which cuts off a single parietal cell and then forms the embryo sac. In a later

[1] Contribution from the Botanical Laboratory of The Johns Hopkins University, No. 8.

paper CAMPBELL ('01) agrees with this description, except that he does not think that there is always in the mature sac a single cell which has the position of a synergid.

That chromosome reduction takes place in the first division of the embryo sac nucleus was indicated by the presence of synapsis before this division in *P. hispidula*, as reported by JOHNSON before the Botanical Society of America at New Orleans in 1905.

CAMPBELL ('01) thinks that the embryo sac of Peperomia is a primitive one, while JOHNSON ('00) considers its peculiar structure as derived. In this paper it will be shown that the embryo sac is made up of the descendants of four nuclei which are apparently the nuclei of four megaspores, and that these nuclei have, by the loss of dividing walls, come to lie in the same cell. Some of the peculiar features of the mature sac are probably connected with this fact.

For the sake of convenience, each of the four species will be described separately, after which the general considerations will be discussed.

Peperomia Sintensii

The material of this species was collected in Jamaica by Mr. W. R. MAXON and identified by M. CASIMIR DE CANDOLLE.

The development of the flower and of the mother cell in the nucellus agrees with that described for *P. pellucida* by JOHNSON ('00). The flower consists of two stamens and a carpel in the axil of the bract. The ovule (*fig. 28*) is single and orthotropus, with a single integument (*fig. 28, i*), which makes its appearance about the time that the tapetum is cut off from the archesporium (*fig. 2*).

The archesporium arises in the apex of the nucellus as a single hypodermal cell (*fig. 1*), which is clearly distinguished from the surrounding cells by its larger size and more densely staining contents. At the micropylar end this cuts off a single parietal cell (*fig. 2*), and then, without giving rise to any other cells, forms the embryo sac. The parietal cell divides first by an anticlinal wall and then by repeated divisions gives rise to a mass of tissue between the embryo sac and micropyle (*figs. 4, 28, t*).

Owing to the scarcity of young material, I was unable to count the chromosomes in the division cutting off the tapetum, but in the tapetum and in the nucellus there were regularly about sixteen chro-

mosomes. This is double the number found in the embryo sac, as will be described later. The chromosomes are small and short, and are therefore readily counted in a cross-section of a spindle at metaphase. *Fig. 2* shows such a section in the tapetum, while *fig. 3* represents a longitudinal view of a vegetative nucleus at a slightly older stage. Up to this time there certainly seems to have been no chromosome reduction, and nothing resembling megaspore formation.

The single sporogenous cell (*fig. 2*) which is left after the cutting-off of the tapetum and which is to form the embryo sac is apparently a megaspore mother cell, as will be shown below. Its nucleus divides to two, four, eight, and finally in the mature sac to sixteen nuclei.

The first division is heterotypic and takes place as follows. The resting nucleus (*fig. 4*) shows a meshwork of linin along which chromatin granules are scattered. In the center of this meshwork is a large clear space containing a large nucleolus. After considerable growth the nucleus goes into synapsis. The meshwork contracts rapidly around, or to one side of, or even at some distance from, the nucleolus, into a mass in which very little detail can be made out. *Fig. 5* represents an early stage of synapsis, while *fig. 6* is probably older. No evidence of a fusion of spirems was seen either before or during the early stages of synapsis.

At the end of synapsis the mass loosens up, and later appears in the form of a spirem, along which single granules are scattered at rather regular intervals (*fig. 7*). The spirem is apparently continuous and becomes loosely coiled, and the granules divide along the longitudinal axis of the spirem. A small portion of such a stage is shown in *fig. 8*. After this the spirem divides longitudinally and the two halves may diverge considerably in places (*fig. 9*), but later they come together again and all apparent traces of the division are lost. While this is taking place, the spirem is beginning to be arranged in loops (*fig. 10*), and is still apparently continuous, the loops being rounded at the ends. It does not seem possible that this appearance can have anything to do with the splitting just described. The looping becomes more pronounced and the spirem segments transversely in such a way that the loops give rise to chromosomes. There are eight of these, the haploid number, and they are apparently formed by the

coming together side by side of parts of the spirem that before were arranged end to end. The chromosomes then contract and show the twisted appearance characteristic of the heterotypic division (*fig. 11*).

After considerable contraction they have the appearance of two irregular rounded masses lying together. Sometimes these are seen to be connected by strands (*fig. 13*), and just before this, when the constituent halves are about twice as long as wide, they are sometimes placed end to end with a constriction between them (*fig. 12*).

It would seem from this that the two halves originally placed end to end in the spirem, then side by side in the loops, again come to lie end to end, and that each half probably represents a chromosome (cf. *fig. 16*). The strands connecting the two halves are often seen to be double (*figs. 12, 13*), and they might always be so if seen in the right plane. Besides this, the halves sometimes show evidence of being double. This may be due, as is often supposed, to the split previously described. Before the spindle is formed the two halves come together, producing somewhat elongated chromosomes (*fig. 14*). About this time the nucleolus begins to fragment and to be thrown out into the cytoplasm. After the spindle is formed (*fig. 15*) the chromosomes divide transversely to their long axes (*fig. 16*). From what has been said it seems evident that this division separates parts of the spirem which were originally placed end to end and that it is therefore a transverse division. This is then the heterotypic and reducing division.

As the chromosomes approach the poles they become crowded together (*fig. 17*) and surrounded by a clear space. While this is going on, the chromosomes lose their distinct outlines and a nucleolus makes its appearance in their midst. While the chromosomes lose their distinct outline and probably also some of their substance, they seem nevertheless to be represented by irregular masses during most if not all of the period between the first and second divisions (*figs. 18–20*). Between the succeeding divisions they seem to go to pieces to a much greater extent (cf. *figs. 22–25*). Before the formation of the spindle, the chromosomes appear as double structures, consisting of two rods lying side by side. It may be that these represent the two halves of the spirem seen in the prophases of the first division.

and that the second division completes the longitudinal separation begun in the first.

The first two divisions differ from those in *P. pellucida* in that there are formed evanescent walls separating the daughter nuclei. When the daughter nuclei of the first division have begun to be organized, an equatorial plate is formed on the spindle (*fig. 17*). This grows until it becomes a wall stretching across the embryo sac (*fig. 18*). The plane of this wall is not constant, but it may extend longitudinally or transversely across the sac, or take any intermediate position, and may also separate the sac into equal or unequal parts (*figs. 18–20*). It persists only for a short time, disappearing before the next division or remaining as a remnant after it (*fig. 21*). There is no trace of it later in the four-nucleate stage. When the two nuclei divide to four, plates are formed on both spindles. One of these never becomes very prominent, but the other forms a wall separating one nucleus from the other three (*fig. 22*). The position of this wall is variable, as was the one in the two-nucleate stage. It may cut off a nucleus at either end or any side of the sac, but generally it appears at the lower end. This wall, like the first, persists for only a short time. It generally disappears before the next division (*fig. 23*), but may persist as a remnant after it. As in *P. pellucida*, the four nuclei assume the position of the nuclei of a tetrad of microspores. The walls just described are apparently megaspore walls. This, however, will be discussed later.

In the next two divisions all of the nuclei divide simultaneously, giving eight, and then in the mature sac sixteen nuclei. The nuclei of the eight-nucleate stage and of the mature sac are arranged about the periphery of the sac (*figs. 24–28*). As in *P. pellucida* (JOHNSON '00), one of the sixteen nuclei becomes an egg, another has the position of a synergid, six are cut off singly against the wall and finally degenerate, while eight fuse to form the endosperm nucleus. *Fig. 29* shows a sac in which fertilization is taking place. Four of the peripheral nuclei are shown, while five others are fusing to form the endosperm nucleus. One of these latter was probably formed by the fusion of two. The other two fusing nuclei, as well as two peripherals, are in another section.

In the division of the four nuclei to eight no cell plates are formed.

Fig. 24 represents a stage in which they should be apparent if present. In the last division (*fig. 26*), cell plates are formed on all the spindles. These give rise to walls cutting off all of the nuclei except those which are to fuse to form the endosperm nucleus, but leaving these eight free in the cytoplasm (*figs. 27, 28*). These walls are thin at first and might be easily overlooked, but later they become much more prominent. In the eight-nucleate stage two nuclei are always found together at the micropylar end (*fig. 25*). The presence of spindles show these to be sisters (*fig. 24*). In the last division one of these gives rise to the egg, the other to the nucleus with the position of a synergid (*figs. 26–29*). The sisters of the egg and synergid fuse with the sisters of the six peripherals to form the endosperm nucleus. As in *P. pellucida* (JOHNSON **'00**) the peripherals are arranged singly against the embryo sac wall (*fig. 29*) and finally degenerate. About the time of fertilization the eight nuclei which form the endosperm nucleus migrate toward the base of the sac and fuse into one large nucleus.

STRASBURGER (**'05**) assumes that owing to their position the polar nuclei in the ordinary angiosperm are not surrounded by cell walls and that their fusion is due to the fact that their development has stopped and that they are in a single cell. This explanation may apply to the eight fusing nuclei in *P. Sintensii*.

A peculiar phenomenon was noted in fertilization. The male and female nuclei at this time are in the resting stage and have one or more cavities with their concave sides facing each other (*fig. 29*). The edges fuse so that a mass of cytoplasm is apparently held in the fusion nucleus (*fig. 30*). The wall around this mass of cytoplasm grows faint and finally disappears.

The mature seed resembles that of *P. pellucida* (JOHNSON **'00**). There is a small oval embryo, while the rest of the sac is filled with a much larger endosperm, which is cellular from the first division. The sac is about the same size as at fertilization, but the cells of the nucellus have become filled with starch to form perisperm.

Peperomia arifolia

The development of *P. arifolia* was followed only as far as the sixteen-nucleate sac.

The development of the flower and of the embryo sac agrees very

closely with that just described for *P. Sintensii.* There is a single archesporial cell which cuts off a tapetal cell and then forms the embryo sac. The tapetum divides as in *P. Sintensii.* The embryo sac nucleus divides to two, four, eight, and finally sixteen nuclei.

The first division is heterotypic and shows the usual synapsis. At this division a cell wall is formed across the sac. This wall is variable in position and generally disappears before the next division, but may persist as a remnant after it. At the second division plates are formed on both spindles. One soon disappears, while the other forms a wall separating one nucleus from the other three. This wall is variable in position, and all signs of it are usually lost before the next division. The next two divisions leave the mature sac with sixteen nuclei.

Peperomia ottoniana

The material of this species was collected in Mexico by Dr. C. J. CHAMBERLAIN. It is very much like *P. Sintensii,* but shows some constant differences. It was identified by M. CASIMIR DE CANDOLLE.

Owing to lack of young material the investigation of this species had to be begun with the four-nucleate stage. There were only three ovules showing a four-nucleate sac, but they are worth recording, as they appear perfectly normal, and seem to throw some light on the problem under discussion.

The youngest sac (*fig. 31*) shows the micropylar nucleus completely cut off from the other three by a very distinct and well-developed wall. This nucleus is much larger than the other three, which are all about the same size. The cell occupied by this large nucleus contains much denser protoplasm than the one containing the other three. The stage just described resembles rather closely the four megaspores of the ordinary angiosperm, where one megaspore is to form the sac while the other three degenerate. The further development, however, seems to be different, and agrees with the two species of Peperomia just described.

The two other four-nucleate sacs which were seen are larger and apparently older than the one just described, and show no sign of a wall separating the nuclei, which are all about the same size (*fig. 32*). The eight nuclei formed from these four show no appreciable difference in size.

The further development resembles very closely that of *P. Sintensii*. The mature sac contains sixteen nuclei. There is one egg and one nucleus with the position of a synergid. Six peripheral nuclei are cut off against the wall of the sac. The remaining eight fuse to form the endosperm nucleus about the time that fertilization takes place. In the fusion of male and female nuclei there was seen no sign of protoplasm being taken into the nucleus, as described for *P. Sintensii*. Many of the stages of this species resemble *P. Sintensii* so closely that one might readily be mistaken for the other.

Peperomia pellucida

The development of the embryo sac nucleus and the structure of the mature sac, as described by JOHNSON, agree with the description just given for *P. Sintensii*. Therefore only the first two divisions of the embryo sac nucleus need be considered here.

The first division is heterotypic and shows about ten or twelve chromosomes. A meshwork contracts and goes into synapsis. This stage is followed by an apparently continuous spirem, which divides into twisted heterotypic chromosomes.

In both divisions plates are formed on the spindles. These plates probably do not develop further, as no larger plates or walls were seen, although a great number of nuclei were examined at stages which should show them if present. These plates probably are the remnants of walls such as have been described for the other three species.

Discussion

As has been said, CAMPBELL ('01) considers the unusual structure of the embryo sac of Peperomia as primitive, and expresses the belief "that the contents of the embryo sac with the sixteen nuclei represent a prothallial tissue and the nuclei are at first entirely similar." JOHNSON ('02), after a study of Peperomia and allied genera, comes to the conclusion that the peculiarities of the embryo sac have been secondarily acquired from the ordinary angiosperm embryo sac.

The present investigation seems to support the latter view. The nuclei of the mature sac of *P. Sintensii*, instead of being similar at first, bear a definite relation to each other. The presence of the reducing division in the primary embryo sac nucleus and the forma-

tion of evanescent walls in the first and second divisions seem to indicate that the sac is composed of the descendants of the nuclei of four megaspores and that the primary embryo sac nucleus is a mother cell and not a megaspore nucleus.

If the walls corresponded to those of prothallial cells, we should expect to find them in the third division, but here not even a cell plate was seen. Besides this, the nearest phylogenetic relatives in which the first divisions of a megaspore result in a cellular structure are found among the leptosporangiate Filicales, where the heterospory is supposed to be of rather late origin, and it does not seem probable that Peperomia has reverted to the characters of an ancestor as remote as one in which we would find the first divisions of the megaspore giving rise to a cellular structure.

This position is strengthened when we consider the four-nucleate stage of the Mexican species. Here the nucleus which is cut off is considerably larger and surrounded by much denser protoplasm than the other three. The resemblance to the four megaspores of the ordinary angiosperm is quite striking.

The presence of the extra nuclei in the mature sac is in harmony with the view that these nuclei are the descendants of four megaspore nuclei.

The nuclei of the four-nucleate sac of Peperomia have the same position with reference to each other as the nuclei of a tetrad of fern spores or of a tetrad of microspores of a spermatophyte. This position is not always apparent when the nuclei are dividing, and as the sac is somewhat rounded it may be that this arrangement is a mechanical response to the physiological conditions.

That four potential megaspore nuclei may be included in a single cell has been shown by CANNON ('00) for *Avena fatua*. Here the four megaspore nuclei may or may not be separated by cell walls, but in either case three degenerate and the other forms the embryo sac. A similar phenomenon is reported by SMITH ('98) for Eichhornia.

The case of Crucianella (LLOYD '02) is interesting in this connection. Here the four megaspores are not separated by walls, but indications of plates are found on the spindles in the divisions of the megaspore mother cell nucleus. According to LLOYD, the four megaspores are physiologically and morphologically similar. Each

nucleus divides to two, but afterward the nuclei derived from the three megaspores nearest the chalazal end degenerate, while those from the one nearest the micropyle form the sac. The condition in Crucianella approaches that in Peperomia, and it may be that the shape of the sac, which is much less elongated in Peperomia than in Crucianella, gives the megaspores a better chance to develop together in Peperomia.

That physiological conditions do play a part in the structure of the embryo sac of Peperomia may be indicated by the fact that while the megaspore nucleus which is cut off by a cell wall is generally at the chalazal end, it is always the one nearest the micropyle which forms the functional egg apparatus.

WIEGAND ('00) reports an evanescent wall in the first division of the embryo sac of Convallaria. Here the mother cell forms the embryo sac directly and this wall may represent a megaspore wall.

That more than one megaspore may possess the potentialities for development is indicated by the number of plants in which more than one has been reported as dividing (COULTER and CHAMBERLAIN '03).

The similarity in the fate of the four megaspores of *P. Sintensii* is striking. Each gives rise to two nuclei of the endosperm and two cut off against the embryo sac wall.

If we were to accept the view of PORSCH ('07) that an egg apparatus represents an archegonium, we might conceive of the embryo sac of Peperomia as really composed of four sacs, each of which gives rise to a single archegonium. The relationship of the nuclei of each egg apparatus, as previously described, is the same as that found in the egg apparatus of an ordinary angiosperm, if we assume that one synergid fuses with the nucleus which usually fuses to form the endosperm, that is, with the sister of the egg, as is the case in the four-nucleate sac of Cypripedium (PACE '08). That there may be in Peperomia four potential egg apparatuses is indicated by the fact that the nucleus of the four-nucleate stage, which is cut off and therefore resembles the functional megaspore of the ordinary angiosperm, does not usually form the functional egg apparatus. It must be remembered, however, that no such similarity in the fate of the megaspore nuclei as has been described for *P. Sintensii* exists in *P. his-*

pidula (JOHNSON '07), where fourteen out of sixteen nuclei fuse to form the endosperm nucleus.

Before applying the theory of PORSCH it may be well to consider the theory itself in its relation to the ordinary gymnosperms and angiosperms. In Selaginella, Isoetes, and the gymnosperms, all of the first divisions of the megaspore are non-cellular, after which there is a number of cellular divisions in all species that form archegonia. It is in the cellular tissue that the archegonia are formed by cell divisions. The first two divisions of the ordinary angiosperm embryo sac are generally homologized with the free nuclear divisions of the gymnosperm prothallus, and the fact that in the derived sac of *P. Sintersii*, where cell walls are formed at the first two or megaspore-forming divisions, there is no sign of even a cell plate at the third or prothallial division, indicates that the character of the free cell divisions in the angiosperms is quite constant. It does not seem probable that nuclei formed in the angiosperm embryo sac by free nuclear division can be homologous with the nuclei in the cellular archegonia of the gymnosperms, for we would have to explain how the archegonia became shifted back from the cellular to the non-cellular phase of the prothallus.

If the above idea is correct, the polar groups in the angiosperm embryo sac can have no such phylogenetic significance as is ascribed to them by PORSCH, but all of the nuclei in the mature sac must be homologous or at least differentiated only in the last division.

From what has been said, it seems possible that in some angiosperms besides Peperomia, in which the embryo sac is not developed from one of a row of megaspores, the first four nuclei of the sac are megaspore nuclei. It must be remembered, however, that in most cases we have no evidence for this, other than the presence of the reducing division in the embryo sac mother cell, and it is a mistake to suppose that the same structure may not come about in plants in more than one way. Besides this, it is hard to see how four embryo sacs can have become merged into one in the large number of cases in which a row of megaspores is not formed (COULTER and CHAMBERLAIN '03) without disturbing the normal number and position of the nuclei, as has been done in Peperomia.

Some workers have been inclined to regard the presence of the

heterotypic division in a cell of the nucellus as the sole criterion for determining that this cell is a megaspore mother cell, and that the first four resulting nuclei are the nuclei of megaspores. This view seems to leave out of consideration the great number of points in the life-history of plants at which reduction may take place, and the evident tendency among vascular plants toward the reduction of sporogenous tissue in the megasporangium and nucellus.

In the Archegoniatae the archesporial cell may give rise to a large mass of tapetum and a considerable number of functional spore mother cells. Since we can trace the reduction of these divisions until among angiosperms the archesporial cell may without dividing form one megaspore mother cell, it does not seem reasonable to suppose that the divisions of the mother cell to four megaspores may not also be left out and the mother cell function directly as a megaspore. In this case the heterotypic division might be pushed forward and take place in the embryo sac.

Among the lower plants this reducing division may take place at almost any point in the life-history and there seems to be no sufficient reason for thinking that it must occur at the same place in all angiosperms.

If the two divisions which form the spores from the mother cell, or one of them, have been left out, we could of course expect to find no evidence of it other than the entire absence of any signs of the division.

In a recent paper on Cypripedium, Miss PACE (**'08**) shows that the sporogenous cell divides once and one of the resulting cells forms the embryo sac, while the other may occasionally divide once. There is not even a sign of a cell plate in the first division of the nucleus which forms the embryo sac. Miss PACE calls the first two nuclei of the embryo sac megaspores, but does not state her reasons for doing so. The question might arise as to whether they are megaspores or whether one division in spore formation has been left out. That the nucleus of the degenerating cell should occasionally divide does not seem surprising when we remember the large number of plants in which the nucleus of a degenerating megaspore may do so.

The writer does not wish to be understood as denying that there are two megaspores in the embryo sac of Cypripedium, or that the

first four nuclei in the embryo sac of any plant in which a row of megaspores is not formed are megaspore nuclei, but simply as suggesting that in most cases we have no adequate proof of this, and that in the present state of our knowledge there is at least one other way in which some of them may be regarded.

The homologies in all these cases may be cleared up by further work. We have, however, no right to push them further than the present evidence justifies, or to suppose that all plants must behave alike in this respect, when we consider the large number of different analogous organs which have been arrived at by very diverse methods.

Summary

The archesporium of the species of Peperomia studied arises as a single hypodermal cell, which cuts off a single parietal cell and then forms the embryo sac directly.

The first division of the embryo sac nucleus is heterotypic. The nucleus goes into synapsis. This stage is followed by an apparently continuous spirem. This splits longitudinally but later the two halves come together again. The chromosomes are formed from loops in the spirem. When these divide, they seem to separate two parts of the spirem which were originally placed end to end.

The second division may divide the chromosomes along the longitudinal split seen in the prophase of the first division.

In the third division of the embryo sac nucleus of *P. Sintensii*, no cell plates were seen on the spindles, but in the last division cell walls are formed on all the spindles. These walls cut off, against the embryo sac walls, one of each of the eight pairs of nuclei, and leave the other eight free in the cytoplasm. These free nuclei fuse to form the endosperm nucleus. The egg and a nucleus with the position of a synergid are cousins. The other six nuclei which are cut off against the embryo sac wall finally degenerate.

The mature sac contains sixteen-nuclei, which are apparently derived from four megaspores. That the first four nuclei of the embryo sac are megaspore nuclei is indicated by the fact that the first division of the embryo sac mother cell nucleus is heterotypic and reducing, and that in *P. pellucida* cell plates are formed on the spindles of the first two divisions, while in *P. Sintensii* and *P.*

arifolia these plates grow into evanescent walls which extend across the embryo sac and separate the nuclei.

We are not justified, however, in extending the conception of four megaspores in an embryo sac to all angiosperms in which a row of megaspores is not formed, because we do not know that the division of the mother cell to megaspores may not be omitted and the place of the heterotypic division be changed.

In the fertilization of *P. Sintensii* some cytoplasm appears to be taken into the nucleus.

NOTE.—Since the above was written, there have appeared two papers dealing with sixteen-nucleate embryo sacs. One is by COULTER,[1] in which he expands a suggestion offered by LLOYD in 1902, that when four megaspores are not formed the first four nuclei of the sac are spore nuclei so far as development is concerned, and says that the formation of megaspore nuclei cannot be omitted.

In a paper on the phylogeny of the angiosperm embryo sac, ERNST[2] describes a sixteen-nucleate embryo sac in Gunnera. Here he finds an egg, two synergids, six antipodals often in two groups of three, and seven nuclei which fuse to form the endosperm nucleus. He then attempts to fit the archegonial theory of PORSCH to Gunnera, and concludes that the egg group represents an archegonium, while two more are represented by the six antipodals together with two of the nuclei which fuse to form the endosperm. He thinks that the other four nuclei fail to form an archegonium, and that the explanation which he gives of the embryo sac of Gunnera may apply to *Peperomia pellucida*. In the case of the embryo sac of *P. Sintensii*, which resembles very closely that of *P. pellucida*, it has already been shown that if we should apply the theory of PORSCH there would be four and not three archegonia. ERNST has not worked out the relation between the nuclei in the embryo sac of Gunnera, and therefore it would seem premature to speculate as to the conditions there, but there seems to me to be no sufficient reason for thinking that the nuclei would represent three rather than four of the archegonia of PORSCH.

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[1] COULTER, J. M., Relation of megaspores to embryo sacs in angiosperms. BOT. GAZETTE **45**:361–366. 1908.

[2] ERNST, A., Zur Phylogenie des Embryosackes der Angiospermen. Ber. Deutsch. Bot. Gesells. **26**:419–437. *pl.* 7. 1908.

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13. WIEGAND, K. M., The development of the embryo sac in some monocotyledonous plants. BOT. GAZETTE **30**:25–47. *pls. 6, 7*. 1900.

EXPLANATION OF PLATES XXXI–XXXIII

All drawings were drawn with the aid of a camera lucida and reduced one-half. *Figs. 1, 2, 4, 18–23, 31, 32* were made with a no. 8 ocular and a 1.5^{mm} objective; *figs. 3, 5–17* with a no. 12 ocular and a 1.5^{mm} objective; *figs. 24–27, 29, 30* with a no. 8 ocular and a $1\frac{1}{2}$ objective; *fig. 28* with a no. 2 ocular and a $\frac{1}{2}$ objective.

Peperomia Sintensii

FIG. 1.—Primary archesporial cell in apex of nucellus.

FIG. 2.—Archesporial cell has divided to sporogenous and parietal cell; the latter dividing and showing sixteen chromosomes; integument beginning to grow up around nucellus.

FIG. 3.—Longitudinal view of an anaphase in a vegetative cell.

FIG. 4.—Nucellus containing embryo sac mother cell, which shows a stage shortly before synapsis; part of integument which now surrounds nucellus shown at base of nucellus.

FIG. 5.—Early stage of synapsis in embryo sac mother cell.

FIG. 6.—Later stage of same.

FIG. 7.—Part of an apparently continuous spirem, just after synapsis.

FIG. 8.—Later stage of same, showing divided granules.

FIG. 9.—Still later stage, showing split spirem.

FIG. 10.—Still later stage; the two halves have come together and the spirem has become looped.

FIG. 11.—Chromosomes derived from loops shown in *fig. 10*.

FIG. 12.—Later stage of same.

FIG. 13.—Still later stage.

FIG. 14.—Still later stage; the two halves have come together.

FIG. 15.—Longitudinal section of a metaphase of the first division of embryo sac mother cell.

FIG. 16.—Anaphase of same.

FIG. 17.—Early stage in formation of daughter nuclei.

FIG. 18.—Two-nucleate embryo sac, showing cross-wall separating the two nuclei.

FIG. 19.—Slightly older embryo sac.

FIG. 20.—Embryo sac showing same stage as last.

FIG. 21.—Nuclei of a two-nucleate sac dividing; remnant of dividing wall still present.

FIG. 22.—Four-nucleate sac; one nucleus separated from the other three by a wall.

FIG. 23.—Later stage; wall was disappeared.

FIG. 24.—Four nuclei have divided to eight; no cell plates on the spindles; the sister nuclei in micropylar end.

FIG. 25.—Later stage; the two sister nuclei still in micropylar end.

FIG. 26.—The eight nuclei have just divided to sixteen; cell plates seen on the spindles.

FIG. 27.—Later stage; cell plates shown in last figure have grown into walls cutting off eight nuclei against the embryo sac wall and leaving eight free in the cytoplasm.

FIG. 28.—A mature ovule; the embryo sac contains sixteen nuclei; *p*, pollen tube with nuclei; *t*, tapetum; *i*, integument.

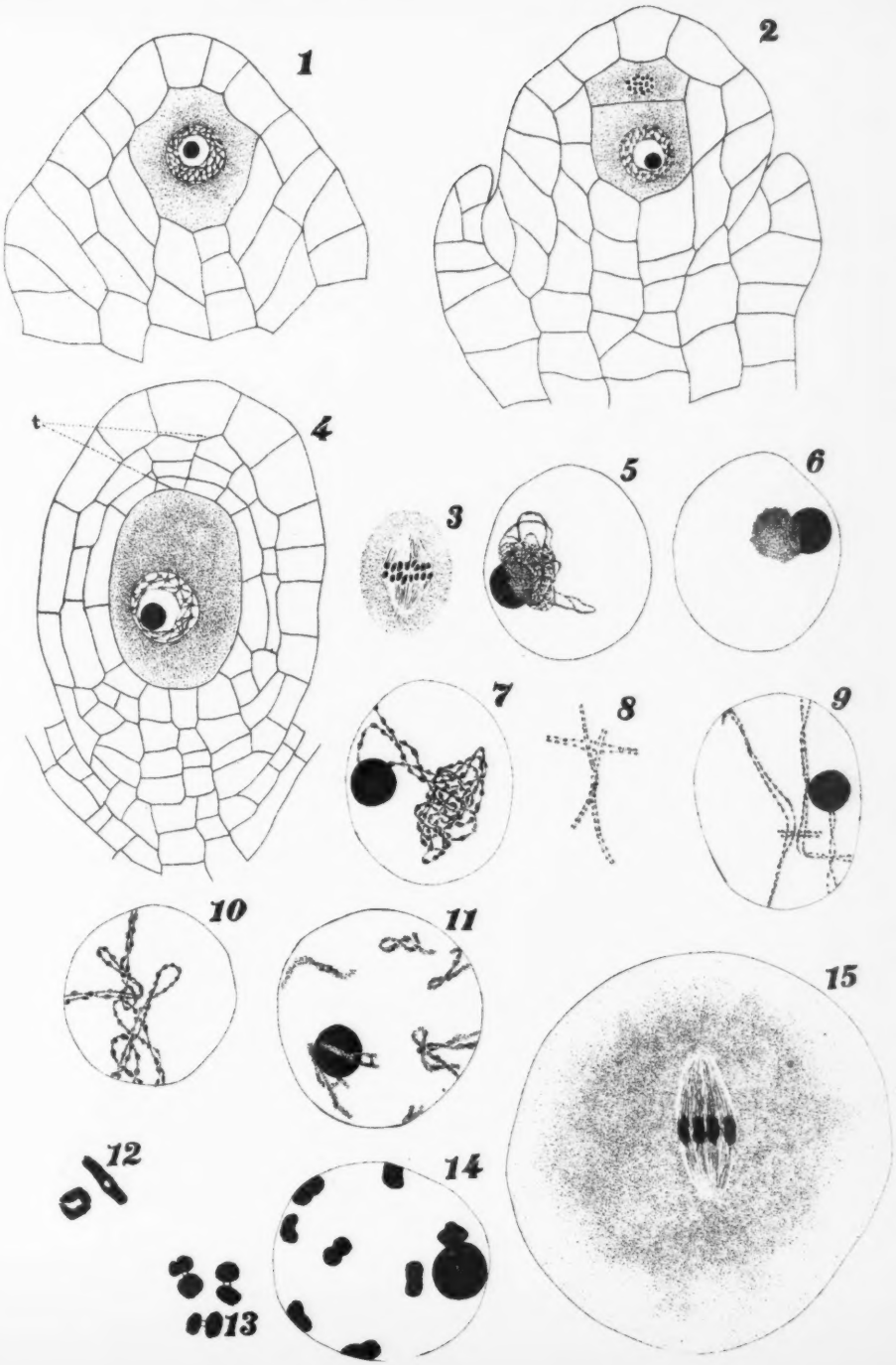
FIG. 29.—Embryo sac with fertilized egg and nuclei fusing to form the endosperm nucleus; *e*, egg with fusing nuclei; *p*, pollen tube; *s*, nucleus with the position of a synergid; *d*, peripheral nuclei which will degenerate; *f*, nuclei fusing to form endosperm nucleus.

FIG. 30.—Later stage of fusion in male and female nuclei.

Peperomia ottoniana

FIG. 31.—Four-nucleate sac; one nucleus cut off and surrounded by dense protoplasm.

FIG. 32.—Later stage; the wall dividing off one nucleus has disappeared.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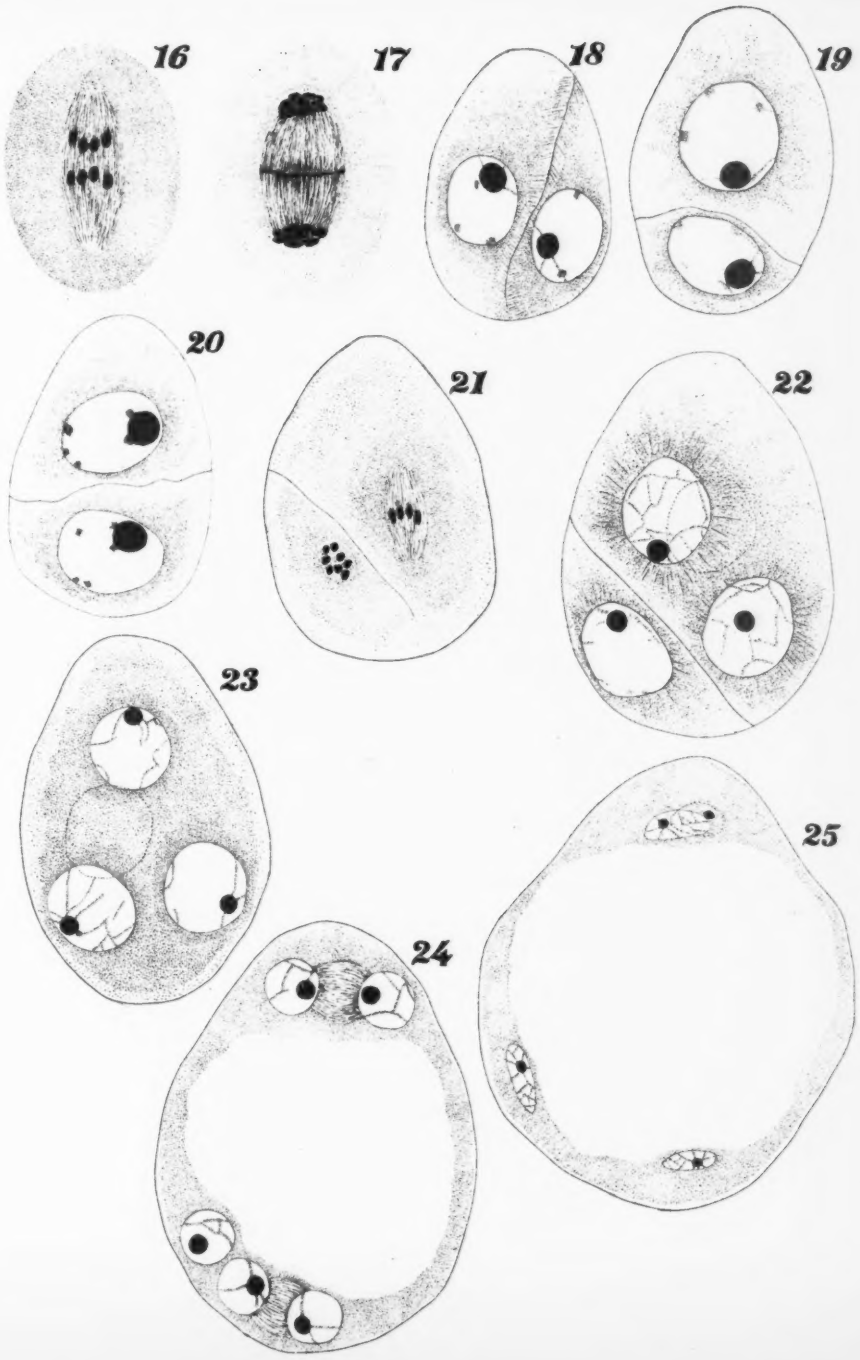
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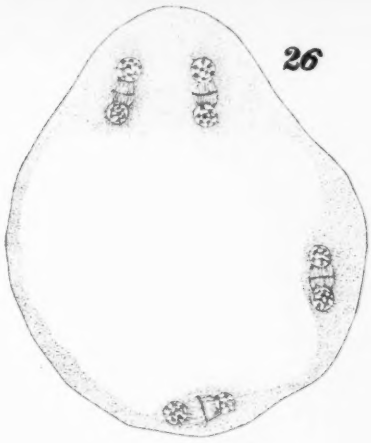
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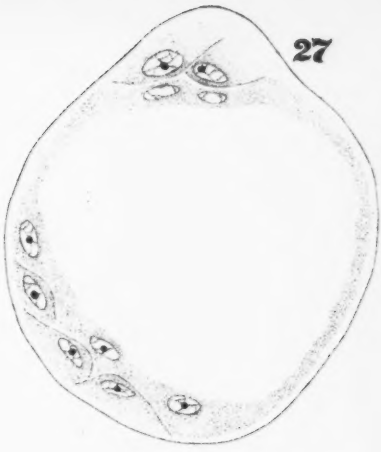
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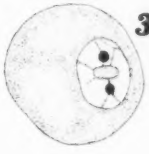
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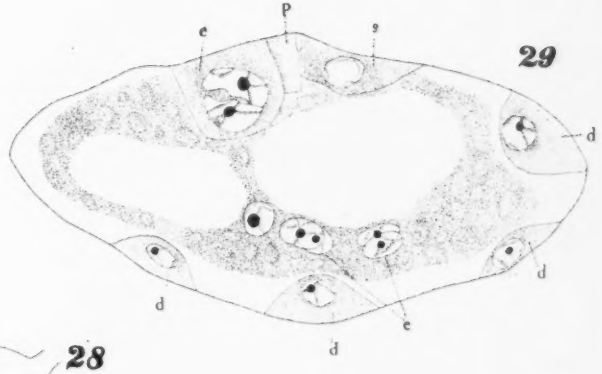
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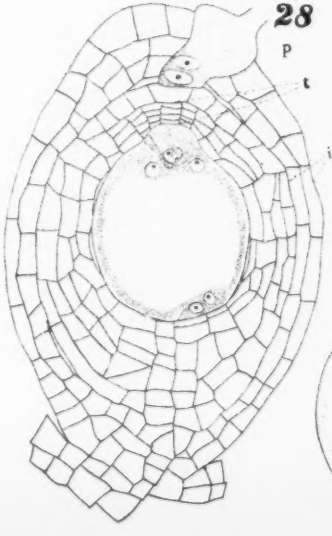
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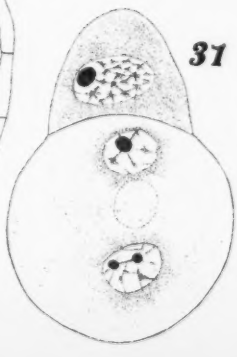
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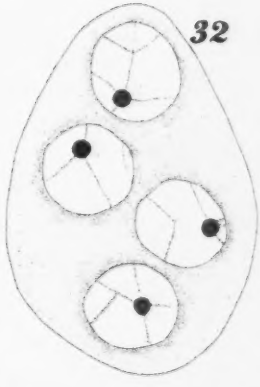
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BRIEFER ARTICLES

A NEW POISONOUS MUSHROOM

(WITH TWO FIGURES)

During last August I received from Dr. O. E. FISCHER, Detroit, Michigan, a few living plants of a species of Tricholoma, which he reports as causing several severe cases of poisoning. The specimens were sufficiently well-preserved for study and diagnosis, also for a photograph, and for casting spores for a photomicrograph. The plants are medium size, white in color with dull clay-colored tinge and stains in places. The plants are moist but not viscid, with the pileus minutely scaly but subtomentose over the center. The scales possess the darker color and under the hand lens some of them appear nearly black, but because of their minute size the dark color is not evident to the eye. The stems are subbulbous, the shape of the bulb being peculiar and resembling that of *Lepiota lenticularis*, which in side view is supposed to suggest the shape of a biconvex lens. The taste of the plants is mild, and no particular odor was observed in those received. The plants appear to be near to *Tricholoma pallidum* Pk. from Worcester, Mass., but differ in a number of particulars, as will be seen by a comparison of the diagnoses.

Before giving the technical diagnosis I quote the following from Dr. FISCHER'S letter:

> I am sending you a set of agarics of unusual interest and importance, for they are the ones that made seven people very ill in Rochester, Mich., on August 21. Violent and hemorrhagic vomiting, diarrhoea, sweating, and some cardiac disturbance were the symptoms, lasting several hours and coming on one hour after eating even of minute quantities. Some of the women are still suffering from intestinal disturbance. None that ate escaped; none died. I have spent considerable time and energy in taking two of the victims to the exact spot where they picked the offenders and got the cause of the trouble. It is a white-spored agaric, growing in open grassy woods on a leafy base, in clusters and groups. I should greatly appreciate a certain identification of this agaric, the more so since it looks, tastes, and smells inviting, and was "O.K.'d" by a member of our club.

Tricholoma venenatum Atkinson, n. sp.—*Plants* 4–8^{cm} high, pileus 4–7^{cm} broad, stem 1–1.5^{cm} thick, plants white with dull clay-colored tinge and stains; *pileus* moist not viscid, convex-expanded, subumbonate,

center fleshy, thin toward the margin, plane or subrepand, minutely scaly with fibrous scales, subtomentose area over center, surface pale buff

FIG. 1.—*Tricholoma venenatum* Atkinson.

to pale clay color, the scales possessing the darker color, under the lens some of them appear nearly black; *gills* adnexed, broadly sinuate, sub-

distant, whitish, thin, dull clay color especially where bruised; *spores* white, smooth, oval to broadly subelliptical, 5–7×3.5–5 μ; *cystidia* none; stems subbulbous with a bulb like that of *Lepiota lenticularis*, fibrous striate, solid, sordid white, becoming in age where handled dull clay color;

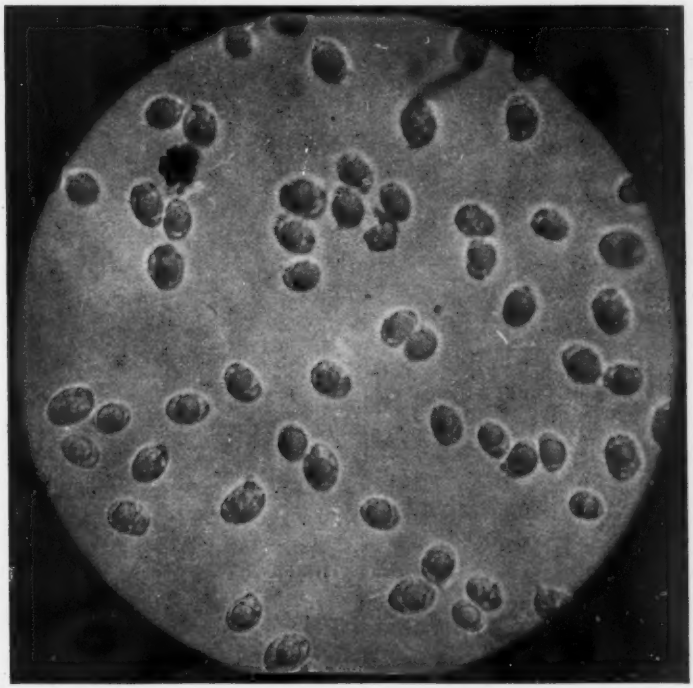

FIG. 2.—Photomicrograph of spores of *Tricholoma venenatum;* Zeiss ocular No. 18, objective 3mm; object 370mm from sensitive plate.

odor and *taste* mild.—No. 22573 C. U. Herb., from Dr. O. E. FISCHER, Detroit, Mich., received August 29, 1908.

(Sporophoro albo, leniter sordide luteo, 4–8cm longo, pileo 4–7cm lato, stipite 1–1.5cm crasso; pileo convexo-expanso, subumbonato, squamulis minutis obducto; lamellis adnexis, late sinuatis, tactu sordide luteis; sporis hyalinis, glabris, ovatis vel subellipsoideis, 5–7×3.5–5 μ; stipite subbulbo, fibroso-striato, tactu sordide luteo.)

GEO. F. ATKINSON, *Department of Botany, Cornell University.*

AFFINITIES OF PHYLLOCLADUS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 121

In connection with the work on *Phyllocladus alpinus* published in this journal (BOT. GAZETTE **46**:339–348. *pls. 20–22.* 1908), it was the intention not to venture upon a discussion of the relationships until a more complete knowledge of the life-history had been obtained from further material. On account of the probable delay connected with securing and investigating the new material, it seems better to present at this time such conclusions as the results already obtained seem to justify.

In 1872 Phyllocladus was placed among the Podocarpineae by STRASBURGER,[1] the relationship being based upon external resemblances. In ENGLER and PRANTL'S *Pflanzenfamilien* it is put among the Taxineae. In 1903 PILGER[2] placed it in a separate group (Phyllocladoideae) intermediate between Taxineae and Podocarpineae; this disposition of the genus being based upon features in which Phyllocladus differs from the Taxineae, namely the two-sporangiate microsporophyll, the uniovulate scale, the arillus, and the anatomy of the vegetative structures. Miss ROBERTSON[3] follows PILGER in assigning to Phyllocladus this intermediate position, with a greater affinity for the Podocarpineae.

In comparing Phyllocladus with the Podocarpineae and with the Taxineae, its relationship to the former tribe becomes very evident. The principal features of resemblance to Podocarpineae, in contrast with the corresponding features of Taxineae, may be enumerated as follows:

1. The microsporophyll of Phyllocladus bears two abaxial sporangia; the microsporophylls of the Taxineae are all of the peltate type, bearing three to eight sporangia.

2. Each scale of Phyllocladus bears one centrally placed ovule; among the Taxineae each scale bears two lateral ovules.

3. The microspores of Phyllocladus have wings, and four or five nuclei at the time of shedding; those of the Taxineae have no wings, and only one or two nuclei at the time of shedding.

4. Male prothallial cells are formed in Phyllocladus and in all the Podocarpineae; none occur in the Taxineae.

5. The evanescent prothallial tissue of Phyllocladus is similar to that found in the Podocarpineae.

6. The megaspore membrane is well developed; this membrane is

[1] STRASBURGER, E., Die Coniferen und die Gnetaceen. 1872.

[2] PILGER, R., Taxaceae. Pflanzenreich, nos. 4, 5. 1903.

[3] ROBERTSON, AGNES, Some points in the morphology of *Phyllocladus alpinus*. Annals of Botany **20**:259–265. *pls. 17, 18.* 1906.

present in all the gymnosperms except the Taxineae, among which it is almost entirely eliminated.[4]

The features in which Phyllocladus resembles the Taxineae and differs from the Podocarpineae are as follows:

1. The ovule is erect; in the Podocarpineae it is more or less inverted, except in *Dacrydium latifolium.*

2. The cladodes contain centripetal wood, according to Miss ROBERTSON (*l. c.*). WORSDELL[5] states that centripetal wood is more common among the Taxineae than in any other group of Coniferales; it has been found in the leaf and cotyledon of Taxus and Cephalotaxus, in the cotyledon of Torreya,[6] and in the stem of *Cephalotaxus koraiana.*[7]

3. The arillus of Phyllocladus originates at the base of the ovule, just as does that of Taxus; the so-called epimatium (PILGER, *l. c.*) of Podocarpus arises from the scale. If this epimatium represents the arillus of Phyllocladus and Taxus, it differs in origin and form; if it does not represent the arillus, it is a structure not found in those genera.

These comparisons indicate that in number and in importance the features of Phyllocladus in common with those of Podocarpineae are much greater than those in common with Taxineae. The winged microspores and the multicellular and evanescent prothallial tissue alone would seem to be of sufficient importance to associate Phyllocladus with the Podocarpineae. We are inclined, therefore, to assign Phyllocladus to the Podocarpineae, thus confirming STRASBURGER'S conclusion of 1872; and not to regard it as referable to Taxineae, or as worthy of constituting a distinct group.—N. JOHANNA KILDAHL, *The University of Chicago.*

NOTE ON THE POLLEN OF MICROCACHRYS

NORÉN[8] has recently described certain of the reproductive features of Saxegothaea. He found that the microspore, like that of the other podocarps recently described, has supernumerary prothallial cells. Unlike the other forms, however, the grains are not winged. In connection with the

[4] THOMSON, R. B., The megaspore membrane of the gymnosperms. Univ. Toronto Biol. Series, no. 4. 1905.

[5] WORSDELL, W. C., On transfusion tissue; its origin and function in the leaves of gymnospermous plants. Trans. Linn. Soc. Bot. London II. **5**:301–319. *pls. 23–26.*

[6] CHICK, EDITH, The seedling of *Torreya myristica.* New Phytol. **2**:83. 1903.

[7] ROTHERT, W., Ueber parenchymatische Tracheiden und Harzgänge im Mark von Cephalotaxus-Arten. Ber. Deutsch. Bot. Gesells. **17**:275. 1899.

[8] NORÉN, C. O., Zur Kenntnis der Entwicklung von *Saxegothaea conspicua* Lindl. Svensk. Bot. Tidskr. **2**:101–122. *pls. 7–9.* 1908.

deposition of the pollen there is a very interesting condition. Sometimes the pollen falls in the micropyle, and sometimes in the cavity around the ovule, whence it grows over the tissues into the micropyle. This recalls the condition of affairs in the Araucarieae, and is essentially similar in this respect to Agathis, as I have found it.

In the pollen of Microcachrys there is a similar excess of prothallial tissue. The grain has wings, however, but not of so definite a character as those of Dacrydium and Podocarpus, which, as is commonly known, bear two well-developed floating appendages. In Microcachrys a large percentage of the grains have three rather poorly developed wings, though the greater number are of the type which is characteristic of the higher members of the group. The winging of the grain is, as it were, in its experimental condition in Microcachrys, and the form is to be considered in this respect as a transitional one between Saxegothaea on the one hand and Dacrydium and Podocarpus on the other.

Attention has often been directed to the biwinged condition of the pollen of the pines and podocarps as an indication of the probable affinity of the two groups. This view is no longer tenable, since the wings of the pollen in the latter are a development within the group itself, analogous but not homologous with those of the pine series. On the contrary, the relationship of the microgametophytic condition in the Podocarpeae to that in the Araucarieae is increasingly apparent.—ROBERT BOYD THOMPSON, *University of Toronto.*

CURRENT LITERATURE

BOOK REVIEWS

North American Uredineae

PROFESSOR J. C. ARTHUR has begun his presentation of the Uredineae in the *North American flora*.[1] No one who has kept informed of our mycological literature, even in the most general way, needs to be told that the author is the leading American specialist on this group of fungi, and that this is the first attempt to monograph the rusts for the whole continent. Heretofore one has had to depend on the restricted paper of BURRILL dealing with the rusts of Illinois, and FARLOW'S *Host index of North American fungi*, on the special papers by ARTHUR, HOLWAY, and others, and on the check lists and *exsiccati* that have been issued from time to time. The need of the work, therefore, cannot be questioned, and no one who has been engaged in a similar task can fail to appreciate the immense amount of effort it has required to bring it thus far toward completion. The part already issued, which includes descriptions of about 150 species and 34 genera, the writer understands to be but the advance guard of two or more parts to be issued later, as the material is worked up.

The monograph is thoroughly well done. It presents a uniform treatment of description and terminology. The bringing together and describing anew all stages, especially the pycnia which have largely been neglected before, make it especially valuable. It also reflects our latest knowledge of the life-history of the various species, to which the author has so long contributed with telling results. As to the real usefulness of the specific keys given under the genera, perhaps there may be some question, but the author no doubt has made them as valuable as they can be made. Mycologists have gone so far in describing new species of rusts (and other fungi as well) chiefly because they occur on new hosts, that one in self-defense acquires the habit of disregarding keys, so far as possible, and uses the host and specific description as the shortest route to identification. Then, too, it is very difficult to discover sufficient morphological characters for use in keys to distinguish the species of a large genus, so that frequently the host genera and families are necessary as characters to fill deficiencies. In his keys ARTHUR has made use of both hosts and morphological characters, using the latter apparently whenever possible.

Aside from the unquestioned merit of the work, the reviewer would dissent strongly from the point of view that compelled the author to split up old genera and to coin many new specific names. These changes did not all appear for the first

[1] ARTHUR, JOSEPH CHARLES, North American Flora.—Uredinales (Coleosporiaceae, Uredinaceae, Aecidiaceae pars) **7**:83–160. 1907.

time in the work under review, but they are all brought together here, and so focus our attention on the ninety (about) specific names (considerably over one-half) that bear ARTHUR'S name as their authority; and he is also responsible for sixteen (about one-half) of the genera. However, he is not quite so extreme in this respect as MURRILL has been in his monograph of the Polyporaceae. ARTHUR has obtained part of his genera from new material and part by splitting up old genera, basing the new genera largely upon their possession of one or more of the O, I, II, III stages characteristic of the rusts. His familiarity with the rusts is such that he is able apparently, if given only the II stage, to tell what other stages it possesses, and so can place it in a genus.

Judging from this past tendency to publish new species under the old recognized genera, a tendency he has not yet entirely lost, I expressed doubt to the late Professor UNDERWOOD, editor of the *Flora*, that ARTHUR would follow his Vienna paper in his treatment of the North American Uredinales. As he did follow it, however, I promptly received from UNDERWOOD the following: "Some time ago you charged that ARTHUR was not possessed of the courage of his convictions in regard to his publication of genera in the Uredinales. I commend to your prayerful attention the second part of Vol. VII of *North American flora*, issued March 6, and move that it is time to have a retraction of that charge." I herewith publicly make that retraction; but what will become of this nomenclature when some ambitious name-juggler revises our rusts fifty years hence, or possibly even after the next botanical congress!—G. P. CLINTON.

NOTES FOR STUDENTS

Turgor and osmotic pressure.—The relation between these stands in great need of accurate study. LEPESCHKIN, a few months ago, discussed the matter before the German Botanical Society.[2] After reviewing the terminology, he designates as turgor and turgescence the condition of tenseness of the tissues due to internal pressure in the cells. For quantitative purposes he defines as a turgor pressure (*Turgordruck*) the total pressure exercised by "cell contents" upon the "cell walls;" but he evidently means by *Zellinhalt* the cell sap, for he explains that the *Zellwände* must be of plasmatic nature. By turgor tension (*Turgordehnung*) he designates the elastic elongation of the walls in any dimension, wrought by turgor pressure. This only partly accords with the best usage in this country, where turgidity rather than turgescence names the condition, and turgor the internal pressure which produces turgidity, while turgor tension has seldom been considered quantitatively. LEPESCHKIN then analyses turgor pressure into four components: (*a*) surface tension (*Zentraldruck*), varying between 0.016 and 1.6 atmospheres, with a variation of 10–12 per cent.; (*b*) swelling of the plasma (*Quellungsdruck*); (*c*) the osmotic pressure of substances dissolved in the plasma; and (*d*) the osmotic pressure of the cell sap and the wall

[2] LEPESCHKIN, W. W., Ueber den Turgordruck der vacuolisierten Zellen. Ber. Deutsch. Bot. Gesells. **26a**: 198. 1908.

liquids. But since neither *b* nor *c*, as the author himself points out, can exercise any effect on turgor pressure, it is difficult to see why they should be reckoned as components. The study of the osmotic pressure of the solutes in cell sap and wall is carried out with a show of mathematical formulae that look formidable, but the data are really not yet adequate for exactness. The experimental results show that the observed osmotic pressure is always less than the calculated, which is due to the greater or less but general permeability of the protoplasts, a feature too much overlooked hitherto, though clearly pointed out by various investigators and *a priori* obvious. The effects of temperature changes, especially between 0° and 20° C., were also examined. A warning against conclusions based on the exclusive use of KNO_3 as a plasmolytic agent without correction for permeability is given.

In a later paper,[3] LEPESCHKIN reports the results of a study of the permeability of the pulvinus cells of Phaseolus and Mimosa, in which this proves to be surprisingly high. The solutes (except sugar) escape so rapidly when the tissues are brought into water, and especially into running water, as to reduce the apparent osmotic pressure (determined by the isotonic coefficient method) by 25 to 50 per cent. A change in the permeability of the plasma membranes may alter the turgor pressure by several atmospheres. LEPESCHKIN proposes to show in another article that such changes really occur (as has been hitherto assumed) under the action of various agents.—C. R. B.

The blood of plants.—PALLADIN'S preliminary paper[4] bears a rather striking title, which will be just enough if the theory proposed is fully established. Certain colorless chromogens, probably products of protein decomposition, have been found in plants, and these become pigments (already familiar to common observation in various discolorations produced on cutting or crushing) under the action of oxygen in the presence of oxidases. These respiratory enzymes are therefore to be considered as pigment producers, and the respiratory pigments doubtless include a number of pigments already known, such as those of the indigo plants. PALLADIN proposes to call all of them, irrespective of their chemical composition, phytohematins, in recognition of the identity of their physiological significance with that of the hematin of the blood. To show this it was necessary to find reductases in plant as in animal tissues, and PALLADIN announces their discovery. These enzymes reduce the respiratory pigments, which then go on down to CO_2, and H_2O, etc. The following scheme shows the relation of the various respiratory processes:

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3 LEPESCHKIN, W. W., Ueber die osmotischen Eigenschaften und den Turgordruck der Blattgelenkzellen der Leguminosen. Ber. Deutsch. Bot. Gesells. **26a**:231–238. 1908.

4 PALLADIN, W., Das Blut der Pflanzen. Ber. Deutsch. Bot. Gesells. **26a**:125–132. 1908.

PRIMARY PROCESSES	SECONDARY PROCESSES
Anaerobic enzymes (zymase, etc.)	Oxygen of the air
↓	↓
Catalase, reductase	Respiratory oxidases
↓	↓
Products of fermentation (alcohol and other substances)	Phytohematins
	↓
	Products of respiration (CO_2, H_2O)

To unify the respiration of animals and plants still further, it will be necessary to show that the oxygen from the air is not combined directly with the hemochromogen, but by the aid of oxidases; and this the recent discovery of these enzymes in the blood renders probable. The behavior of the colorless blood of the lower animals and the sap of plants is quite similar, according to this view.

It is not to be supposed, however, that oxygen does not have other relations than to the chromogens; but these are neglected in the above scheme, which may be taken as only a partial representation of respiratory processes. In fact the more the matter is studied, the more complex and diversified appear the chemical changes subsumed by the word respiration.—C. R. B.

Fungi and hemicelluloses.—In the hope of obtaining some insight into the action of fungi on their hosts, SCHELLENBERG[5] has investigated the behavior of a number of species, which can be cultivated on media of known composition, in respect to their decomposition of hemicelluloses. Those used were several, the products of whose hydrolysis was known. *Molinia coerulea* among the grasses, *Lupinus hirsutus* among the Leguminosae, *Phoenix dactylifera* among palms, *Impatiens Balsamina* and *Cyclamen europaeum* with an amyloid reserve, and *Ruscus aculeatus* among the lilies furnished the hemicelluloses. On hydrolysis they yield respectively dextrose and xylose, galactose and arabinose, galactose and mannose, galactose and xylose, mannose and a little arabinose. A large number of fungi were tested. To explain their action, which he finds strictly specialized and very different from that on true celluloses, SCHELLENBERG has to assume the existence of at least four different enzymes, which he calls the Molinia, the Lupinus, the date, and the amyloid enzymes. Study of their behavior on dead and living plant parts permits similar conclusions. Thus fungi may be used to eliminate hemicelluloses from celluloses in unlignified tissues. The effect of fungi in the destruction of the plant constituents in the soil is probably much more important than has been believed hitherto.—C. R. B.

Jurassic plants.—SEWARD[6] has published the results of his study of collections of Jurassic plants from Caucasia and Turkestan, sent by the Comité Géologique de Russie. The Caucasian collection contains representatives of the

[5] SCHELLENBERG, H. C., Untersuchungen über das Verhalten einiger Pilze gegen Hemizellulosen. Flora **98**:257–308. 1908.

[6] SEWARD, A. C., Jurassic plants from Caucasia and Turkestan. Mém. Comité Géol. Russie N. S. **38**:1–48. *pls. 1–8*. 1907.

following groups; Equisetales (an Equisetites), Filicales (a species each in Marattiaceae, Osmundaceae?, Schizaeaceae, and Cyatheaceae?), Bennettitales (a Williamsonia), Ginkgoales (a Baiera), and Coniferales (a Pagiophyllum); in addition to these, there are four unassigned cycadophytes and two species of Podozamites. The collection from Turkestan includes approximately the same range of forms, adding a species of Dipteridinae and eight species of unassigned Filicales, but showing no Marattiaceae or Schizaeaceae; representing Ginkgoales by two species of Ginkgo; and adding three Coniferales. In conclusion, the relations of these floras to those of other regions are shown by a table; and also the wide distribution of some of the species. Among the striking facts are the existence of so many species for a considerable time during the Mesozoic; the general uniformity in the composition of both the Rhaetic and Jurassic floras in different parts of the world; and the remarkable paucity of cycadean remains in the Turkestan beds.—J. M. C.

Light perception.—ALBRECHT has examined a large number of the endemic plants of northern Germany for the organs of light perception (lenticular epidermis, ocelli, etc.) to which HABERLANDT attributes the capacity of distinguishing differences of light intensity. He finds[7] the organs very rare, and when they are present, nearly as common on the under as on the upper surface of the leaf, though it is clear that to the illumination of the upper surface alone is due the exact placing of the leaf in the fixed light position. No difference appeared in the adaptation of sun and shade leaves to the perception of light. He adduces again the experiments made by coating leaves with water, gelatin, and oil, as evidence against HABERLANDT'S theory. After the reading of the paper, HABERLANDT spoke of the faulty methods in all the latter experiments, describing a mode of coating a part of the leaf with water and leaving the other part dry. On stimulating the two parts with light from different directions, the dry part was always the controlling one, even though the light was much weaker. HABERLANDT considers these experiments (to be detailed later) quite decisive. It may be pointed out, however, that other factors than light are here operative and that the weight of evidence is clearly against HABERLANDT.—C. R. B.

Invertase of the date.—VINSON has studied further[8] the invertase of greenr and ripe dates, in an endeavor to discover the reason for its inextractability from the green fruit. He finds that the tannin present does not make it insoluble, nor can it be extracted from ground pulp, so that impermeability of the cell membranes is excluded. He proposes the theory "that green date invertase and possibly other endoenzymes are held in an insoluble combination by some constituent of the protoplasm. In some cases this combination may be broken

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[7] ALBRECHT, G., Ueber die Perception der Lichtrichtung in den Laubblättern. Ber. Deutsch. Bot. Gesells. **26a**:182–191. 1908.

[8] VINSON, A. E., The endo- and ektoinvertase of the date. Jour. Am. Chem. Soc. **30**:1005–1020. 1908. Cf. earlier paper, BOT. GAZETTE **43**:393. 1907.

down and the enzyme pass into solution while the protoplasm is living, but in others the combination may persist, even after the death of the protoplasm. The enzyme may be rendered soluble also by external chemical or physical influences. These probably act by destroying the integrity of the cell and allowing the contact of substances which have been localized in the living protoplasm. On maturity of the tissues the enzyme is generally liberated, possibly by autodigestion or other profound change in the protoplasm."—C. R. B.

Fixation of free N.—HANNIG, holding that HILTNER'S statement as to fixation of free nitrogen by *Lolium temulentum* rested upon objectionable methods of experimentation, has reinvestigated the matter and confirms the latter's results.[9] About 100 per cent. increase in N of the crop over that in the seed is reported with the fungus-infested plants when N was excluded from the culture; whereas there was practically no increase in fungus-free plants. This is claimed to be the first demonstration of the fixation of free N by ectotrophic mycorhiza.—C. R. B.

Zeitschrift für Botanik.—On account of repeated and continued misunderstandings between the publisher of the *Botanische Zeitung* and its editors, FRIEDRICH OLTMANNS and GRAF ZU SOLMS-LAUBACH, the editors will sever their connection with that journal December 31, 1908, and, assisted by L. JOST, will found a new journal, *Zeitschrift für Botanik*, which will be published by Gustav Fischer of Jena. The journal will be a monthly, in the form of the BOTANICAL GAZETTE, and will contain both original investigations and critical reviews. The subscription price is 24 marks.

CO_2 from dead tissues.—NABOKICH reports in a preliminary paper[10] that CO_2 is given off by dead seeds and seedlings of various plants, no matter how killed. He is apparently oblivious of the fact that COPELAND has already described the same phenomenon in dead water plants,[11] and BECQUEREL in seed coats.[12]—C. R. B.

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[9] HANNIG, E., Die Bindung freien atmosphärischen Stickstoffes durch pilzhaltiges *Lolium temulentum*. Ber. Deutsch. Bot. Gesells. **26a**:238–246. 1908.

[10] NABOKICK, A. J., Ueber die Ausscheidung von Kohlensäure aus toten Pflanzenteilen. Ber. Deutsch. Bot. Gesells. **26a**:324–332. 1908.

[11] COPELAND, E. B., Chemical stimulation and the evolution of carbon dioxid. BOT. GAZETTE **35**:81–98, 160–183. 1903.

[12] BECQUEREL, PAUL, Recherches sur la vie latente de graines. Ann. Sci. Nat. Bot. IX. **5**:193–320. 1907.

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